

# Open Research Online

---

The Open University's repository of research publications  
and other research outputs

## The Relevance of Mycorrhizal Research to Conservation and Development Strategies in Semi-Arid Environments

### Thesis

#### How to cite:

Pease, Arnold Paul (2002). The Relevance of Mycorrhizal Research to Conservation and Development Strategies in Semi-Arid Environments. The Open University.

For guidance on citations see [FAQs](#).

© 2002 The Author

Version: Version of Record

---

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data [policy](#) on reuse of materials please consult the policies page.

---

[oro.open.ac.uk](http://oro.open.ac.uk)

**The Relevance of Mycorrhizal Research to Conservation and Development  
Strategies in Semi-Arid Environments**

**a thesis**

**submitted by**

**Arnold Paul Pease B.A. B.Sc.**

**for the degree of B.Phil**

**Department of Biological Sciences, The Open University**

**May 13, 2002**

DATE OF SUBMISSION: 13 MAY 2002

DATE OF AWARD: 5 AUGUST 2002

ProQuest Number: 27919424

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent on the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



ProQuest 27919424

Published by ProQuest LLC (2020). Copyright of the Dissertation is held by the Author.

All Rights Reserved.

This work is protected against unauthorized copying under Title 17, United States Code  
Microform Edition © ProQuest LLC.

ProQuest LLC  
789 East Eisenhower Parkway  
P.O. Box 1346  
Ann Arbor, MI 48106 - 1346

## **Acknowledgements**

I wish to thank my supervisors, H.Denny and I.Ridge, for their guidance, support and encouragement. Also J.M.Barea for alerting me to the importance of mycorrhizas, P.Harris for the initial literature search, F.S.S.Magingo for briefing on his work and on Tanzania, and various members of my family for help with word processing and layout.



## Abstract

Semi-arid regions have traditionally supported substantial human populations but have seen their integrity and productivity seriously compromised by over-exploitation when population growth has coincided with extended droughts. Symbiotic relationships between plants and soil microorganisms are particularly important in nutrient-poor, drought-stressed environments, but are undermined when drastic reduction in plant cover exposes fragile soils to erosion or crusting, leading to desertification. In such conditions, revegetation may fail unless plants and microsymbionts are restored together.

A century of mycorrhizal research has begun to shed light on some of the key organisms and processes operating in undisturbed soils, but knowledge is still extremely sketchy. Little is known of the factors determining the distribution of particular fungal species, though some cope with disturbance better than others, and consequently the fungal species composition tends to change when land is cultivated. Undisturbed natural vegetation, particularly the rhizospheres of healthy trees, is likely to contain propagules of a mixture of effective AM species, together with a range of other soil microorganisms which may also have important symbiotic roles, and thus be a good local source of inoculum for tree nurseries. Munro *et al* (1999) advocate an inoculation strategy based on this insight. Their procedure could be implemented in village tree nurseries, and this is strongly recommended

Savanna-type ecosystems are resilient in the face of drought. Agroforestry mimics these natural ecosystems, and is popular as a way of protecting and improving the productivity of semi-arid land. A range of suitable species is profiled, but the main criterion should be local interest and demand.

Researchers in Senegal identified two AMF species associated with *Faidherbia albida* at a depth of 34 m. Deep-rooting trees are key elements in dryland ecology, and experimental investigation of the possible role of *Glomus fasciculatum* and *Gigaspora margarita* as inoculum for tree seedlings is suggested.

## Table of Contents

<b>INTRODUCTION .....</b>	<b>1</b>
<b>1. DRYLAND ECOLOGY.....</b>	<b>4</b>
1.1. SEMI-ARID REGIONS .....	8
1.1.1. <i>Mediterranean-type ecosystems</i> .....	12
1.1.1.1. <i>The Mediterranean Basin</i> .....	13
1.1.1.2. <i>California chaparral – a fire climax</i> .....	17
1.1.2. <i>Savannas</i> .....	19
1.1.2.1. <i>The role of fire in savannas</i> .....	24
1.1.2.2. <i>The miombo woodlands of Central Africa</i> .....	27
1.1.2.3. <i>Human adaptations of savanna</i> .....	29
1.2. DISCUSSION .....	31
<b>2. DESERTIFICATION .....</b>	<b>34</b>
2.1. THE PHENOMENON .....	34
2.2. THE PROCESS .....	37
2.3. DISCUSSION .....	39
<b>3. MYCORRHIZAS.....</b>	<b>41</b>
3.1. ARBUSCULAR MYCORRHIZAS .....	41
3.2. ECTOMYCORRHIZAS .....	44
3.3. DISTRIBUTION OF THE MAJOR TYPES OF MYCORRHIZA .....	46
3.4. INTERACTIONS BETWEEN MYCORRHIZAL FUNGI AND OTHER SOIL MICROORGANISMS .....	52
3.5. THE MYCORRHIZAL ECOLOGY OF DROUGHT-STRESSED ECOSYSTEMS .....	56
3.5.1. <i>Vertical distribution of AM fungi</i> .....	58
3.5.2. <i>Mycorrhizal dependency</i> .....	60
3.5.3. <i>Survival strategies</i> .....	62
3.5.3.1. <i>Evidence from Australia, Somalia and Spain</i> .....	63
3.5.3.2. <i>Evidence from the American West</i> .....	66
3.5.3.3. <i>Dormancy and re-emergence</i> .....	67
3.6. SUMMARY .....	70
3.7. DISCUSSION .....	72
<b>4. THE SEARCH FOR SOLUTIONS .....</b>	<b>76</b>
4.1. KONDOA AND THE HADO PROJECT .....	77
4.2. 'MORE PEOPLE, LESS EROSION' .....	79
4.3. "THRESHOLDS OF IRREVERSIBILITY" .....	80
4.3.1. <i>North Africa</i> .....	81
4.3.2. <i>Chile</i> .....	83
4.3.3. <i>Southeast Spain</i> .....	86
4.3.4. <i>A low-cost method of mycorrhizal inoculation</i> .....	89
4.4. DISCUSSION .....	91
<b>5. PLANTS AND SYMBIONTS WITH A POTENTIAL ROLE IN ANTI-DESERTIFICATION STRATEGIES .....</b>	<b>94</b>
5.1. ACACIAS.....	95
5.1.1. <i>Acacias on the desert margins of Africa</i> .....	95
5.1.2. <i>Other indigenous African acacias</i> .....	99
5.1.3. <i>Australian acacias grown as exotics</i> .....	102
5.1.4. <i>Acacias and the recovery of degraded dryland</i> .....	104
5.2. OTHER SAVANNA TREES .....	105
5.3. TREES OF THE MIOMBO DRY FOREST.....	115

5.4. AM FUNGAL PARTNERS .....	125
5.5. DISCUSSION .....	127
<b>6. CONCLUSIONS .....</b>	<b>130</b>
6.1. GENERAL DISCUSSION .....	130
6.2. HOW STRONG IS THE EVIDENCE? .....	137
6.3. RECOMMENDATIONS TO DEVELOPMENT AGENCIES AND NGOS .....	140
<b>REFERENCES :.....</b>	<b>143</b>
<b>APPENDIX 1 - PROTOCOL FOR SIMPLE, LOW-COST MYCORRHIZAL INOCULATION .....</b>	<b>160</b>
<b>APPENDIX 2 - SUGGESTIONS FOR FURTHER RESEARCH.....</b>	<b>163</b>

## Table of Figures

<b>Figure 1.</b> Semi-arid, arid and extremely arid regions.....	9
<b>Figure 2.</b> Degrees of aridity in Africa, Asia and Australia.....	10
<b>Figure 3.</b> Degrees of aridity in America.....	11
<b>Figure 4.</b> Dynamics of evergreen sclerophyll shrublands along environmental gradients.	15
<b>Figure 5.</b> Distribution of AM and EM forests of the world.....	47
<b>Figure 6.</b> Kondoia Eroded Area of Tanzania.....	78
<b>Figure 7.</b> Excavated root system of <i>Acacia senegal</i> growing in low sand dunes at Ed Dumokia, Kordofan Province, Sudan.....	99

## Introduction

Mycorrhizas are symbiotic associations between plant roots and soil fungi, involving recognition, response and the development of linking structures through which the controlled exchange of nutrients and sugars is effected. These associations are very ancient, and the plant and fungal partners are thought to have co-evolved over geological time (Smith & Read, 1997). This implies that the current symbioses in natural ecosystems are the product of dynamic adaptive processes attuned to slow geological change and presumably also to the much more rapid climatic fluctuations.

Undisturbed dryland ecosystems have evolved stable mycorrhizal communities (Bethlenfalvay *et al*, 1984), in which both plants and fungi have effective survival strategies for coping with long periods of drought. However, rapid and catastrophic desertification has been widely observed in areas where prolonged and recurring drought, together with excessive grazing and other human pressure, have combined to deplete vulnerable vegetation and soils so seriously as to render the damage apparently irreversible (Le Houérou, 1996), reducing the land to an unproductive condition in which it is unable either to sustain a human population or, by natural processes, to return to its appropriate climax vegetation within a human timescale.

The symbiotic fungi cannot survive indefinitely in the absence of plant hosts, so 'irreversible desertification' may be a condition in which loss of vegetation has led not only to serious loss of topsoil but also, crucially, to the effective absence of the fungal partners without which vegetation could not be restored.

SE Spain has a very long history of desertification, and findings in a representative area chosen for a programme of revegetation (in the Sierra de Filabres, Almería) suggest that levels of mycorrhizal fungi present in the soil are inadequate to support an extensive revegetation programme, even one based on the dominant woody legume, *Anthyllis cytisoides*, (Requena *et al*, 1996). It seems possible that this may be an extreme example, and that intermediate desertification situations may be more common, i.e. where vegetation is degraded and topsoil is eroding, but where appropriate mycorrhizal fungal propagules are still present in useful concentrations in at least some parts of the threatened area. It is of particular interest to establish whether this is so in endangered savanna regions of Africa and elsewhere, where the livelihood of millions of people is at stake.

The present review will attempt to formulate, from the wealth of recent mycorrhizal research, recommendations which would contribute to the effectiveness of measures designed to protect or improve semi-arid land threatened by desertification.

The questions of interest in this study are:

- (a) To what extent is the 'irreversibility' of desertification due to the depletion of mycorrhizal propagules and other soil microorganisms?
- (b) Is the problem the same in areas where desertification is very recent?
- (c) Can desertification be halted or reversed by the outplanting of mycorrhizally inoculated trees or shrubs?
- (d) If so, what plants, fungi and nursery processes can be recommended?
- (e) What further research questions arise?

This study will review the climatic stresses and ecology of drylands, and the current understanding of desertification, before considering the role of mycorrhizas in drought stressed ecosystems and in dryland reclamation. There are several types of mycorrhiza; the main focus will be on arbuscular mycorrhizas, AMs, (frequently referred to as VAM), because the majority of plants in arid and semi-arid areas are endo- rather than ectomycorrhizal. Brief reference will also be made to ectomycorrhizas (EMs), as a number of important tree species in the Mediterranean basin and in the Central African dry forests are ectomycorrhizal.

## 1. Dryland ecology

Low rainfall or intermittent drought necessarily limit productivity, though undisturbed dryland ecosystems have developed efficient coping strategies, and the semi-arid areas (Figure 1) of special interest in this study, and now under threat, have supported substantial human populations.

Aridity is a consequence of one or a combination of the following factors;

- geographic distance of continental land mass from the ocean;
- rain shadow effects;
- subtropical anticyclones (Shmida, 1985).

The core of the hot desert regions is between latitudes 20 and 25° north or south (the Sahara and the deserts of Arabia, Thar, Namibia, Kalahari, central Australia and Peru). These regions are characterized by rainfall which is not only low or extremely low, but also very variable and unpredictable, and which coincides with high temperatures and often with strong winds too, so that evapotranspiration rates are very high.

Temperate deserts and semi-deserts are found between latitudes 30 and 45° north or south. All except Patagonia lack sea contact, and some are high altitude plateaux; these latter have very cold winters and high temperature amplitudes. The western sectors of the Asian drylands, which are at a relatively low altitude, receive remnants of Atlantic precipitation, mainly in winter, with a maximum in March. The central Asian areas, on the other hand, have very dry winters; their rainfall comes in the form of summer storms from the east,



spring vegetation is therefore lacking, the brief growing season beginning after the first summer rains (West, 1983).

Mediterranean-type climatic regions also occur between latitudes 30 and 45° north or south. They are related to oceanic cold currents on the west side of continents, and are characterized by long dry summers and wet winters, which are mild except where altitude brings cold conditions. Autumn to spring/early summer is therefore the season for plant growth, and evaporation losses are less than they would be if the main rains fell in the hot season.

Meigs, (cited by Shmida, 1985, and Dick-Peddie, 1991), proposed the following formula for the classification of arid environments:

E = extremely arid	a = no marked season of precipitation
A = arid	b = summer rain
S = semi-arid	c = winter rain

followed by 2 digits; the first indicates mean temperature of coldest month, the second indicates mean temperature of the warmest month:

0 = <0 °C

1 = 0 – 10 °C

2 = 10 – 20 °C

3 = 20 – 30 °C

4 = >30 °C

E.g. Namibia = Ea 22, Gobi Desert = Ab 04, Burkina Faso = Sb34.

Aridity is a function of low or extremely low precipitation, often combined with desiccating conditions such as high temperature and/or strong winds; summer rainfall in the desiccating winds of the Sahel will infiltrate less, and be less effective, than the same amount of winter rainfall in Mediterranean areas. The Aridity Index (AI) is the ratio of actual precipitation to potential evapo-transpiration (P/PET). The World Atlas of Desertification (UNEP, 1992) recognizes the following categories;

- Hyperarid .....  $P/PET < 0.05$
- Arid .....  $0.05 < P/PET < 0.20$
- Semi-arid ..  $0.20 < P/PET < 0.50$ .

Using these criteria;

- **arid regions** are understood as those with a mean annual precipitation up to 200 mm in winter rainfall areas, or 300 mm in summer rainfall areas, together with a variability of 50-100%,
- **semi-arid regions** have highly seasonal rainfall regimes, with mean annual precipitation of 200 – 500 mm in winter rainfall areas, or 300 – 800 mm in summer rainfall areas, together with a variability of 25 – 50%.

Dryland communities are therefore adapted to long periods of severe water deficit, interspersed with either regular (seasonal-annual) or random periods when water becomes available. To cope with these conditions, plants have evolved different survival strategies. Ephemeral annuals are a prominent feature of arid environments; a rainstorm triggers rapid germination, growth and flowering, and in such conditions species such as *Boerhavia*

*repens* can complete their life cycles within the space of a few weeks, setting and dispersing seed before the soil dries out again. Perennials have a variety of strategies for coping with drought; some have long tap-roots which give them access to deep water tables (e.g. *Acacia tortilis*), others drop their leaves (e.g. *Adansonia digitata*) or die back to ground level and store their resources underground (e.g. *Stipa tenacissima*), others again conserve water by a variety of physiological and structural mechanisms, including succulence combined with CAM metabolism (e.g. *Agave americana*).

Leguminous trees and shrubs, often thorny and of sparse habit, are the most important arboreal groups in many subtropical deserts and savannas. Low shrubs and perennial grasses are also prominent elements in the vegetation (Shmida, 1985). Many arid habitats are saline, and halophytes (particularly of the Amaranthaceae, Aizoaceae, Portulacaceae and Tamaricaceae families) are among the most characteristic genera common to both desert and coastal regions (Shmida, 1985).

Soils of arid regions are usually slightly acid to alkaline in the surface horizon, and commonly contain accumulations of calcium carbonate and sometimes of soluble salts, gypsum or free silica. There is considerable variability, with a wide range of particle size and mineralogy. Some have shallow subsurface zones of clay accumulation. Very sandy soils are extensive in the semiarid tropics; medium and fine-textured soils are extensive in eastern Africa, India and South America. Biological activity is commonly low, as are levels of organic matter, since decomposition is rapid, and this leads to poor aggregation and low aggregate stability and, consequently, to high potential for wind or water erosion.

There is also a tendency for drop impact or sediment deposition to lead to the formation of crusts that decrease infiltration and increase runoff. Shallow soil depth to a cemented horizon is also widely found (Hendricks, 1991).

### **1.1. Semi-arid regions**

The extent of semi-arid regions is shown in Figures 1, 2 and 3, taken from Dick-Peddie (1991) and from Shmida (1985). These derive from Meigs (1953), and are in fact the same map; Figure 1 gives a clearer overview; the semi-arid areas (horizontal shading) have most productive potential to lose from desertification, and the broad band stretching across from the Sahel to Ethiopia and down through Kenya into Tanzania will be of particular concern in this study. But Meigs' code in Figures 2 and 3 provides highly significant information on temperature range and precipitation pattern. For instance, the small 'c' indicating that the main precipitation is in the cooler season (the mediterranean climatic pattern) occurs not only in coastal areas adjacent to cold ocean currents, but also all along the North African coast and into Iran and Turkestan. Europe is not shown, but semi-arid areas of Spain and other European Mediterranean countries would be typically Sc23/Sc13, depending on altitude.

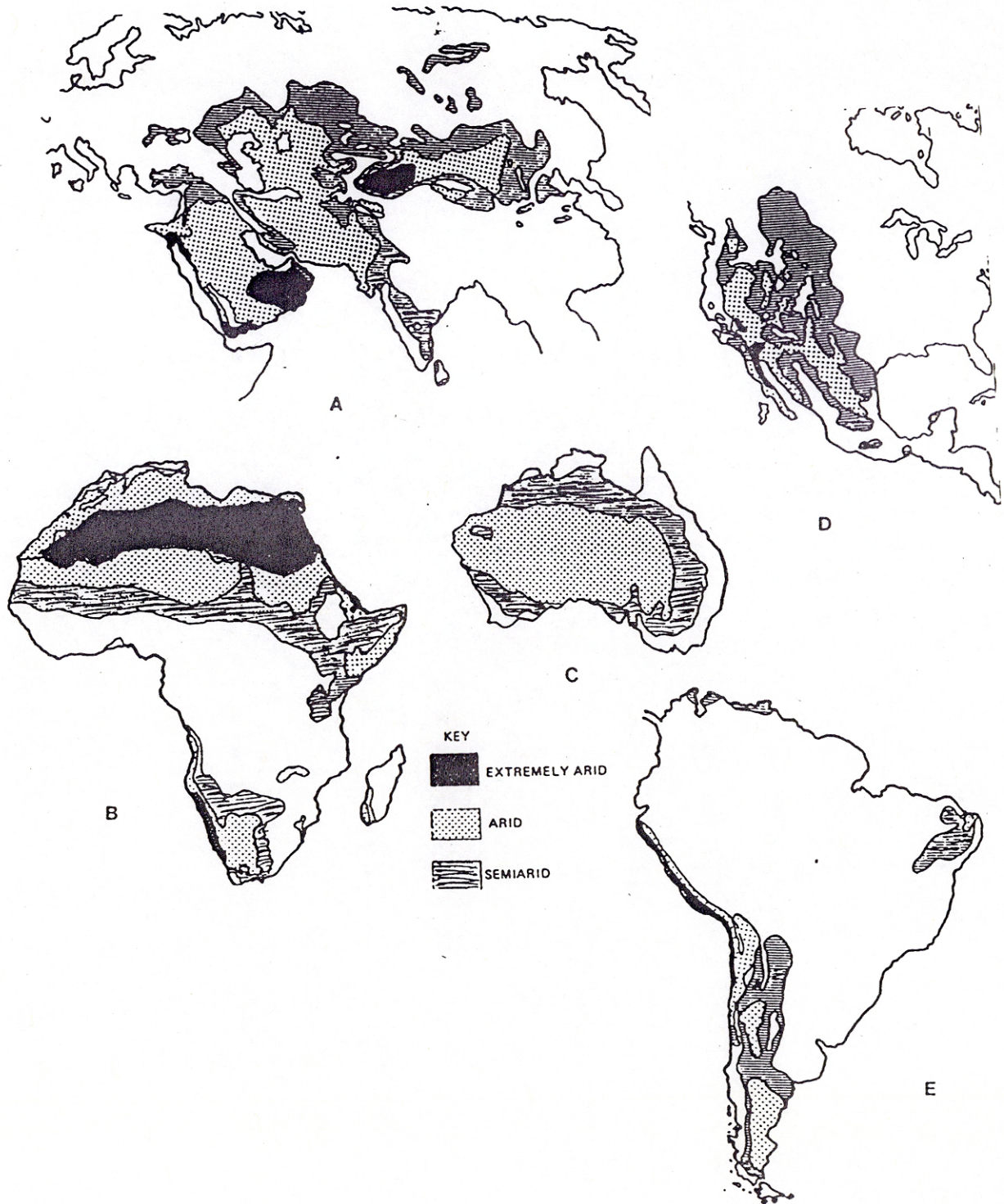
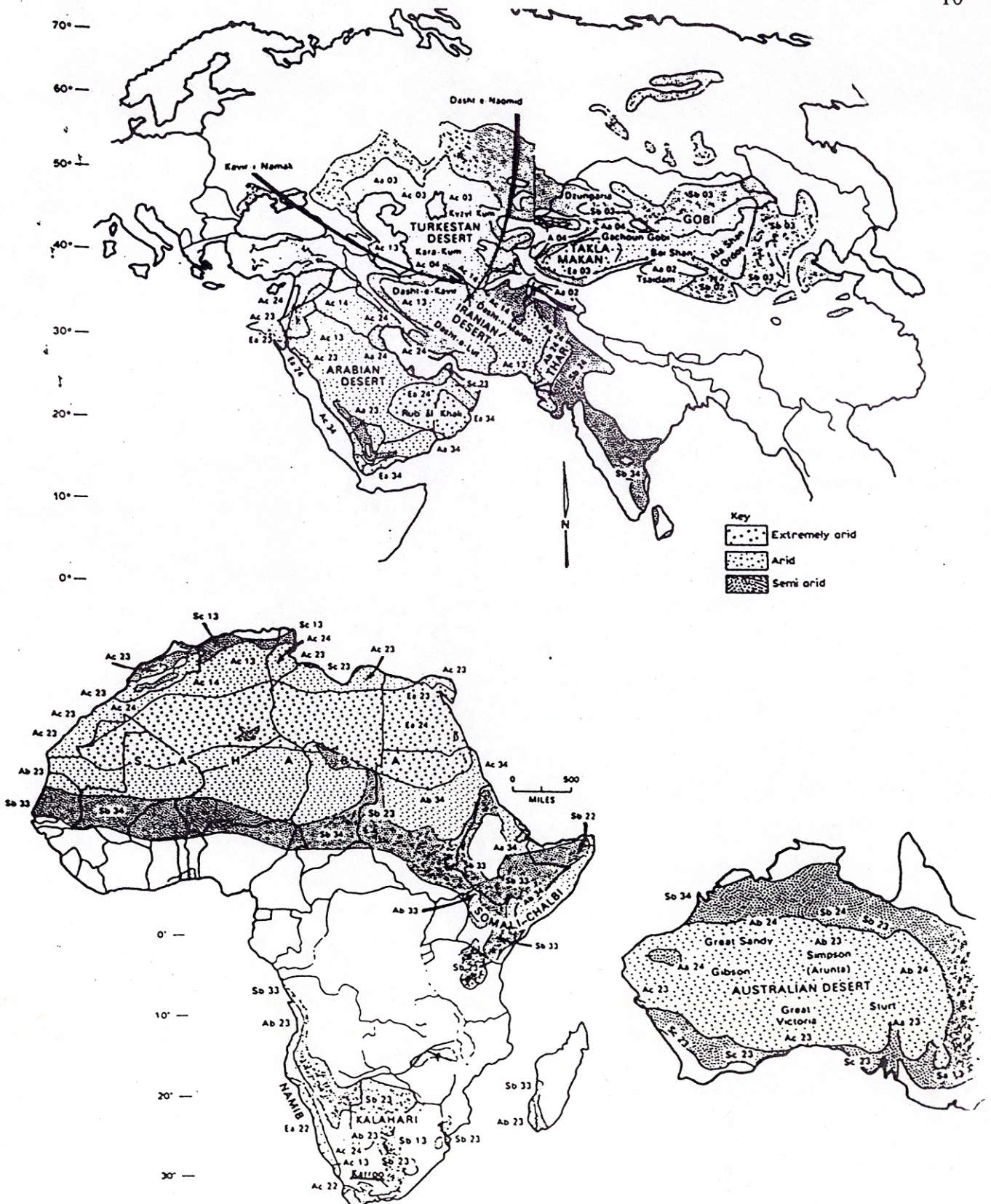


Fig. 1. Semi-arid, arid and extremely arid regions of the continents: A, Asia; B, Africa; C, Australia; D, North America; E, South America. (From Dick-Peddie, 1991, after Shmida, 1985).









**Figure 3.** Degrees of aridity in America  
(from Shmida, 1985, based on the classification and formulae of Meigs, 1953).

Bush fire is an important and recurring factor in many semi-arid areas. Indeed, there are actual fire climax ecosystems, but more often it appears to be a case of adaptations which enable the system to cope with this additional stress factor. Deliberate firing of bush to improve grazing is a traditional management strategy in many savanna areas.

In the following pages two types of semi-arid ecosystem, mediterranean and savanna, are described. These have much in common, as is discussed in Section 1.2., and knowledge accumulated in one may cast useful light on the other.

### **1.1.1. Mediterranean-type ecosystems**

These are typically Sc23 in Meig's code, and are described by di Castri (1981) as transitional between moist and arid ecosystems, and between temperate and tropical regions. There is always a dry season in summer, but its duration is unpredictable. Rainfall occurs typically as heavy, isolated storms, but its timing and annual total is also unpredictable (Clark, 1996).

In Australia and South Africa, the mediterranean-type areas are flattish, commonly with nutrient-poor soils developed from old parent material, further impoverished by leaching and podsolization. In the Mediterranean Basin, California and Chile, on the other hand, the underlying geology is relatively young, and offers a very rolling topography, with high, sharp mountains near the coast, and a mosaic of old and new soils, mostly of low nutrient status (Clark, 1996), but which can locally be moderately fertile (di Castri, 1981). In such conditions, aspect and altitude give rise to a mosaic of microenvironments. Soil



temperature ranges differ widely; in central Chile and California, di Castri recorded a thermic fluctuation of 45-5 °C at 2 cm depth on an equator-facing slope, whereas on a pole-facing slope at 32 cm depth the temperature was stable at 10-15 °C all year round (di Castri, 1981).

#### **1.1.1.1. The Mediterranean Basin**

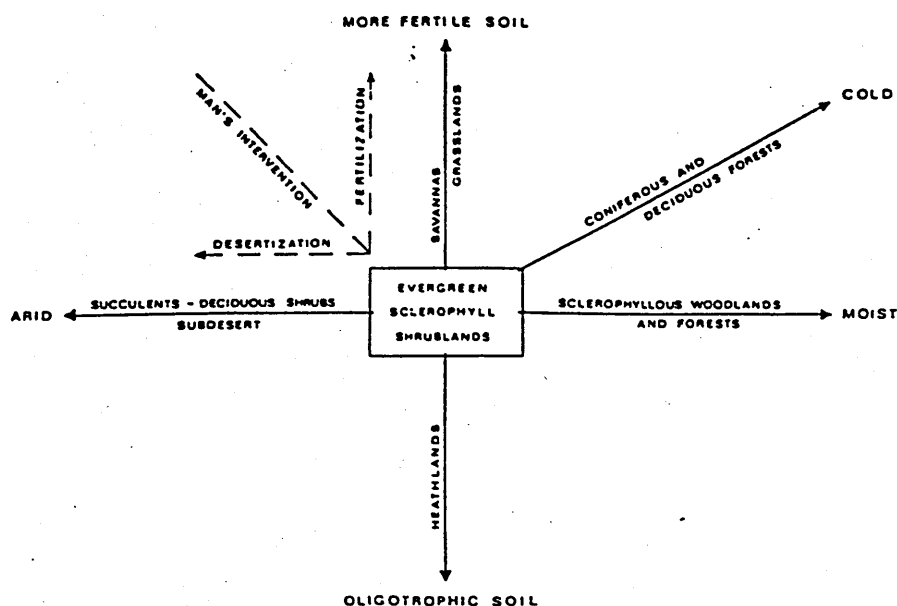
Mediterranean lands have been subject to several paleoclimatic changes, and the mosaic of different environments has offered refugia to plant species surviving from tropical or temperate formations of different geological eras. This has contributed to the species-richness of these areas. Climate rather than substrate is the key factor determining mediterranean vegetation type (Rivas-Martínez, 1987; Clark, 1996), but substrate has a role, and the calcareous soils that are widespread on the limestone rocks forming much of the parent material are particularly associated with the characteristic vegetation of evergreen sclerophyllous shrubs, sometimes with an overstorey of small trees, with or without an understorey of annuals and herbaceous perennials, variously termed maquis, matorral, chaparral or mallee ( Specht, 1981; di Castri, 1981). Quézel (1981) notes that maquis vegetation reaches higher altitudes on calcareous substrates than on metamorphic substrates in the same region, but suggests that its limits are about 1500 m at latitude 30° N and 300-400 m at 45° N.

The Mediterranean Basin has been exposed to long-lasting and pervasive human influence; some ecosystems represent different stages of man-induced degradation, others may be a recovery phase; a few may be close to climax (di Castri,1981; Tomaselli,1981). Pons

(1981) considered that maquis-type vegetation may have existed locally there, in special edaphic environments, but became widespread chiefly due to increased human pressure, though concurrent climate change may also have contributed to its spread.

Mediterranean maquis is fire-prone and fire-tolerant. Deliberate firing has been used for the last 4,000 years to get better and earlier pasture growth and browse (Le Hou  rou, 1981). For example, *Quercus coccifera* regenerates by suckers and stem sprouts after fire, and the protein-rich young shoots are favoured by sheep and goats. Trabaud (1981) considers it to be partially fire-dependent, pointing out that seedlings are rarely observed. In contrast, *Pinus halepensis* regenerates only by seed, disseminated by cones which burst and scatter seed during fire, producing a profusion of seedlings. It seems clear that fire facilitates the regeneration of such species, and that other species have adaptations which enable them to survive fire, though it may be going too far to ascribe fire-dependency to this Mediterranean maquis, unlike its Californian chaparral equivalent, which appears to be an obligate fire-climax system (Hanes, 1981).

Figure 4 (taken from di Castri, 1981) relates this maquis vegetation form to the key environmental gradients – moisture, temperature and nutrient status – which impinge upon it, showing the direction of vegetational change which could be expected with climatic change or human intervention.



**Figure 4.** Dynamics of evergreen sclerophyll shrublands along environmental gradients determined by increased or decreased aridity, increased or decreased soil fertility, and increased control by low temperatures. (from di Castri, 1981).

Tomaselli (1981) subdivides maquis vegetation into :

- high (height >2m), middle (height >0.6 <2 m), or low (height <0.6m);
- dense, discontinuous or scattered.

At the top end of the scale, high dense maquis can be almost impenetrable. Examples in SE Spain have as dominants *Olea oleaster* and *Ceratonia siliqua*, with *Quercus coccifera*, *Pistacia lentiscus*, *Rhamnus lycioides* or *Chamaerops humilis*; *Pinus halepensis* may also establish itself. In W Morocco, dominants are again *Olea oleaster* and *Ceratonia siliqua*, with *Tetraclinis articulata*, *Argania spinosa* and *Pistacia lentiscus*. Kummerow (1981) reports interesting studies by Oppenheimer (1957) on the penetration into rock of root structures of *Pistacia lentiscus* and *Ceratonia siliqua* and extraction of water from rock.

At the lower end of the scale, low discontinuous maquis is frequent as a degraded state in Spain and other Mediterranean countries, and scattered maquis is found in all regions subjected to intensive grazing, especially by sheep.

The two main elements of Mediterranean vegetation are evergreen sclerophyllous shrubs or small trees on the one hand, and winter annuals together with herbaceous and deciduous species on the other (Clark, 1996). Together, these elements form a resilient community able to make the best of the unpredictable climate and of environments resulting from perturbations such as grazing, fire or sporadic cultivation. The annuals are opportunist and take up nutrients rapidly; they use water lavishly but fix carbon rapidly, particularly in early morning, when vapour pressure deficit is still comparatively low, so their water-use efficiency can be high; later in the day they may partially or completely close their stomata. The evergreen sclerophyllous species, on the other hand, photosynthesize at lower rates over longer periods of the day and in some cases, very slowly, throughout the year; though they fix carbon more slowly, they have low rates of water loss, so they too have a high water-use efficiency. Clark (1996) points out that the two elements directly benefit each other, the shrubs providing a favourable microclimate for the annuals and the cover of annuals beneath the shrubs improving soil structure and infiltration and lowering soil surface temperatures.

In the west of Spain and parts of Portugal, management has produced a stable open savanna based on comparatively rich annual grassland and scattered evergreen trees, mainly cork

oak (*Quercus suber*). The density of tree cover can be as low as two to three per hectare (Clark, 1996), though 40/50 trees/ha is probably more usual (Joffre & Rambal, 1993).

The eastern part of the Mediterranean Basin has the longest history of human impact, and saw the domestication of many of our staple food plants – cereals, pulses and fruits, e.g. *Triticum* spp (wheat), *Cicer arietinum* (chick-pea), *Olea europaea* (olive). It has also been the centre of dispersal of annual weeds, which have been introduced into all the other mediterranean-climate regions of the world.

#### **1.1.1.2. California chaparral – a fire climax**

This section is based on Hanes (1981). California chaparral is dominated by evergreen shrubs, usually having small, broad, thick and leathery leaves with stomata confined to the lower surface. These leaves do not wilt; they withstand severe water stress without damage or death. Being evergreen, they are ready to resume photosynthetic activity as soon as environmental conditions allow; indeed, several species fix carbon throughout the year, though dry season dormancy is normally to be expected.

The topography of chaparral areas is commonly steep, resulting in shallow, unstable soils. Fire and summer drought are thought to have shaped California chaparral over the last two million years, and may have played a leading part in speciation. The fire season is from June to December, when high temperatures, dry continental winds and low humidity cause the vegetation to become very dry. Fires can be expected every 10 to 40 years. Temperatures reaching 700° C kill non-sprouting species, produce a nutrient flush and open

up the soil surface to light, stimulating the germination of refractory seeds and sprouting of lignotubers of many shrubby species. Bacteria and fungi are more abundant in burned than unburned chaparral soils. Initially a profusion of ephemeral herbs and forbs may dominate the burn site, species found on burn sites but not elsewhere. In N California these give way to grasses in the fourth or fifth year. Ultimately, the brush overstorey re-establishes dominance, and light, phytotoxins, seedbed conditions or herbivores become limiting (seven to nine years after fire). The herbaceous flora then becomes rare or absent, but it will have left a seedbank ready to take advantage of the next fire.

At this stage, the dominants are woody pioneer shrubs, notably nitrogen fixing species such as those of the genus *Ceanothus*; many of these species are comparatively short-lived, and die out as the stand ages but, like the ephemeral herbs, they leave their seed and will reappear after the next fire. It is worth noting that 8 species belonging to the genus *Ceanothus* were among 25 actinorhizal species (typically pioneer species of *Ceanothus*, *Alnus*, *Casuarina*, *Myrica*, *Comptonia* which form nitrogen-fixing nodules with actinomycetes of the genus *Frankia*) (Brock, 1994), sampled extensively in 16 sites in western USA, and also in Japan and England; all were found to be both nodulated and mycorrhizal (Rose, 1980). Some of these sites are within the general area in which chaparral occurs, so it appears likely though not certain that *Ceanothus* in chaparral vegetation is normally mycorrhizal. This would mean that AMF are adapted not only to the stresses of a mediterranean climate (summer drought and low and unpredictable rainfall at other times), but also to periodic bushfire and a cycle in which a particular host plant genus is present at one stage but absent in the latter years of the cycle.

About half the shrubby species found in California chaparral are able, after burning, to resprout from the swollen lignotuber just under the surface; fire activates numerous buds there which grow into vigorous sprouts. This can occur within weeks after burning, drawing on nutrient and water resources stored in the root system. First year regrowth is rapid. These species can survive many cycles of burning and regrowth and will be increasingly prominent as the chaparral stand matures.

A feature of chaparral shrubs is their extensive root system in proportion to the size of the plant. They have a dual root system; an extensive lateral system and a deeply penetrating system used during summer drought – root depths of over 100 cm and lateral root growth of 60 cm have been reported in three month old *Ceanothus* seedlings. Many dominant chaparral shrubs lack root hairs and are abundantly mycorrhizal.

### **1.1.2. Savannas**

The broad band of semi-arid land south of the Sahara, stretching right across Africa from Senegal to Ethiopia and down into N Tanzania and shown in Meigs' classification as Sb34/Sb23/Sb33 is typical savanna. Like mediterranean-type ecosystems, savannas are transitional, situated along the middle sectors of a moisture gradient. This is particularly clear in Africa, where a central lowland moist forest region straddles the equator and is surrounded on three sides by concentric bands of moist savanna, drier *Acacia* savanna and finally semiarid regions abutting on three deserts (Sahara, Somali Desert and Namib) (Sinclair, 1983).

Savannas have an important and continuous grass stratum, usually with scattered trees and shrubs. The main growth patterns are associated with alternating wet and dry seasons, and bush fires are a characteristic feature. At the wettest end of the savanna gradient the savanna is only maintained against encroaching forest by heavy human pressure, including regular firing, and the result is a forest/savanna mosaic. As rainfall decreases along the moisture gradient, savanna woodland takes over, trees and shrubs forming a light canopy, open enough to allow grasses to flourish. Further decreases in rainfall produce, first, a vegetation with only scattered trees and shrubs, then a shrub savanna, and finally a grass savanna in which trees and shrubs are generally absent (Bourliere & Hadley, 1983). These transitions are of course complicated by factors such as altitude, local topography and drainage (Lawson *et al*, 1968; Vesey-Fitzgerald, 1963).

Savanna vegetation may be a product of natural causes or of human activity. Bouliere and Hadley (1983) argue convincingly that natural climax savannas must be ancient, since plants (most obviously the characteristic and dominant shade-intolerant C<sub>4</sub> grasses) and animals now found only in savannas cannot have originated mainly in closed tropical forests or desertic steppes. They suggest that human activity probably extended areas of existing savanna rather than created a new ecosystem. Human activity has long been a major factor in African savanna. Bush fires can be caused by lightning, but fire has regularly been used by hunter gatherers and pastoralists to create or maintain areas of savanna and, in particular, to clear areas of old or dead, nutrient- poor, herbage and to encourage a flush of young nutritious growth; such man-maintained savanna soon reverts to woodland if protected from bush fires.



Tropical savanna regions receive very high solar radiation, which commonly peaks late in the dry season, leading to very high temperatures. Most tropical savannas have annual mean temperatures  $>20^{\circ}\text{C}$ , and means of  $>28^{\circ}\text{C}$  are extensive in the Sahel. Mean minimum temperatures of the coldest month are in the range  $13\text{--}18^{\circ}\text{C}$  (Nix, 1983).

Seasonality of rainfall is increasingly pronounced along the gradient of decreasing moisture; at the wet end average annual rainfall is 1000-1500 mm., with a short dry period; at the dry end it is  $<500$  mm, characteristically falling in a short rainy season of one to two months. Unpredictability of amount and timing of rainfall also increases along this gradient (Nix, 1983).

Change and instability are important aspects of tropical savanna ecosystems. The present interglacial period, the Holocene, is not climatically stable. The changes of climate are evident from fluctuations in proportions of arboreal and non-arboreal pollen in sediment cores, and it appears likely that the boundaries of rainforest, savanna and desert have fluctuated considerably in quite a short space of time. In the Lake Victoria region, pollen diagrams show mainly grass pollen with a few Fabaceae in the period 15,000 to 12,500 B.P., suggesting savanna, followed by a period of similar length during which forest trees became much more abundant, followed again by further fluctuations (van der Hammen, 1983).

Savannas have a fairly simple structure, and perturbation of one of the dominant species can have far-reaching repercussions. Trees and grasses, usually antagonists in other

biomes, generally coexist harmoniously in savannas; in the Sahel, herbaceous vegetation recovers much more quickly after drought in areas where shrubs and trees have not been cut down. Moderate herbivore pressure will shift the savanna equilibrium in favour of grasses or woody plants, depending on dietary preferences; heavy herbivory will extinguish perennial grasses and push the savanna towards woodland (Bourliere & Hadley, 1983).

There are some interesting aspects of the relationship between woody plants and the herbaceous layer in semi-arid ecosystems such as savanna. The shading effect of the canopy has been shown to be beneficial to the herbaceous layer in Kenyan savanna; lower soil temperatures and greater soil fertility were associated with higher herbaceous productivity in the canopy area than beyond it (Belsky *et al*, 1989, 1993). Visual observation suggested that this effect was common to many trees in the area under study, but the investigation focussed on *Acacia tortilis* and *Adansonia digitata*. Surprisingly, these two very different species, one a legume with a deep taproot as well as shallow lateral roots, often non-deciduous, the other a shallow-rooting deciduous species with a large above-ground water storage capacity, had a comparable positive effect on the productivity of the herbaceous layer which they sheltered.

The shallow roots of dryland trees can extend far beyond the canopy. In the Sahel, *Acacia seyal* had plenty of long lateral roots of 10 m or more in length (Seghier, 1995), and in low sand dunes in the Sudan *Acacia senegal* was found to have lateral roots extending for 25 m and then turning sharply downwards (Wickens, 1998) (cf. Fig. 7). Stone and Kalisz

(1991) report an astonishing rooting radius of 46 m for *Adansonia digitata*, citing Fenner (1980).

Stone and Kalisz (1991) have assembled data showing that many woody species are capable of developing very deep roots. They produce 30 references indicating roots in contact with water tables at depths ranging from 1.5 to 35 m, point out that extractable P concentrations sometimes increase with depth, and suggest that the relative contribution of deeper soil layers to water and nutrient uptake may be greater than has commonly been assumed.

A 'hydraulic lift' mechanism has been proposed for certain deep-rooted plants, water being taken up during the night by taproots from the water table or the deep soil layers just above it and released by shallow roots back into superficial soil. This water is then reabsorbed during the next day, enabling the plant to maintain high transpiration rates during dry periods and also, importantly, supplying water to shallow-rooted neighbouring plants (Canadell *et al*, 1996). Experiments by Caldwell and Richards (1989) showed that isotopically labelled water fed to deep roots of *Artemesia tridentata* appeared in stems of neighbouring tussock grasses within 11 hours. Dawson (1993) reported the same phenomenon in *Acer saccharum* during a drought period in a temperate region. It is not known how widespread the phenomenon is, but it seems likely to be a major factor in the ecology of savannas and other drought-prone ecosystems. It might well help to explain the beneficial effect of *Acacia tortilis* on its understorey, mentioned above, but leaves the equally beneficial effect of *Adansonia digitata* unaccounted for.

### 1.1.2.1. The role of fire in savannas

The deliberate firing of savanna is a practice thought to go back at least 50,000 years in Africa, and to be very ancient in Australia too (Gillon, 1983; Gillison, 1983).

At the wet end of the savanna moisture gradient (rainfall over 1200 mm), a study of the effects of deliberate annual burning over a period of 50 years was conducted at an experimental site in the Olokemeji Forest Reserve, Nigeria, in a border moist forest/derived savanna zone. Where fire was excluded, the forest rapidly re-established itself, and after 28 years only one species of savanna grass (the shade-tolerant *Andropogon tectorum*) was present. Annual burning at the beginning of the dry season, when the moisture content of the grasses and forbs is still high, has a fairly light impact; burning is only partial, and fire temperatures are comparatively low. Thirty years into the Olokemeji experiment, the site that had experienced annual early-burning had developed into a savanna woodland with a very high tree density, and it was increasingly difficult to carry out the annual burning; however, on the late-burn site forest regeneration was being virtually prevented, late burning consumed 84% of the herb layer, and recorded fire temperatures were much higher (Hopkins, 1965 & 1983).

In general, burning creates a flush of available nutrients, but nitrogen present in the plant material is assumed to be largely lost by volatilization. Studies conducted in Olokemeji and in other sites in Southern Guinea (high grass) savanna and Northern Guinea (one moderately low-grass and one woodland site) indicated that nitrogen was completely volatilized from both early and late-burned vegetation, but that grass production in most

Nigerian savanna areas was more or less stable, suggesting that as much nitrogen must enter the system as was lost from it, the suggested routes being rain and fixation by blue-green algal crusts, legume associations and possibly grass-*Spirillum lipoferum* associations (Isichei & Sanford, 1980).

Another long-duration experiment comparing the effects of annual light (early dry-season) burning, annual severe (late dry-season) burning, and complete protection from fire was started by the Northern Rhodesia Forest Department in 1933 in an area of *miombo* woodland with an annual rainfall averaging 1200 mm and a dry season of 6 months. After 23 years, the protected plot showed progressive thickening up of its understorey and increased invasion of evergreen lianas whereas the early-burnt plot maintained regeneration of its woody cover. The late-burnt plot, on the other hand, showed a cumulative effect of burning; the woody cover was increasingly opened up, with a consequent increase in grass growth providing more fuel for fiercer fires, until by 1945 the flames roared up to canopy level during the annual burn.

Burning was associated with a flush of available phosphorus in the soil, but as at Olokemeji it did not appear to affect nitrogen status. Nor, surprisingly, was any difference in organic content found; this was uniformly very low, with no accumulation of organic matter from litter in the early-burnt and the protected sites. It was concluded that the numerous termite colonies present were consuming or removing most of the litter. In this respect, burning did not appear to have deleterious effects on the soil, but it was observed that excessive burning exposed bare soil to the rains, leading to compaction of the surface soil and the

development of a shallow sheet-erosion pattern on sloping ground (Trapnell, 1959; Trapnell *et al*, 1976).

Large-scale grass fires are more frequent in areas moist enough to produce a large amount of grass fuel, but seasonally dry enough to allow it to burn quickly. In the Serengeti, over 60% of the long grass areas in the north west (with annual rainfall averaging 900 mm) were burned annually, usually in the first dry month, whereas only 19% of the drier short grass plains to the south-east were burned in any one year (Sinclair, 1975). Fires are much less common in Sahelian savannas, where sparse ground vegetation limits the spread of fire, but recovery time after fire is longer in such savannas, since most grass species there are annual. In general, infrequent fires are more destructive than annual ones (Gillon, 1983).

The rise in temperature during the passage of grass fire is very brief. The highest temperatures occur at a height of about 50 cm. Inside a burning tussock, temperature maxima are variously quoted in the range 52 to 65° C, and temperature increases are minimal or non-existent at three to five centimetres below the soil surface (Gillon, 1983). It seems likely that actual fire damage to mycorrhizas is minimal, and that the abrupt cessation of photosynthesis impacts on the mycorrhizal ecology of an affected area merely as an intensification of the dry seasonal stress to which the ecosystem is adapted. Mycorrhizal cycles of dormancy followed by recolonization when the next rainy season occurs appear not to be greatly affected.

### 1.1.2.2. The *miombo* woodlands of Central Africa

These woodlands are prevalent in areas with a pronounced dry season, over a wide range of altitudes and precipitation totals (from 500-1200 mm/year in Tanzania) (Trapnell *et al*, 1976), and are of considerable interest both for the role of fire in their maintenance and succession patterns and for their mycorrhizal ecology.

Boaler and associates (Jeffers and Boaler, 1966; Boaler, 1966; Boaler and Sciwale, 1966) describe *miombo* vegetation in Tanzania as consisting of two main layers: a fairly open canopy and a mainly grassy layer, plus an understorey of smaller trees and sometimes shrubs. The grasses can reach heights up to about two metres. The crowns of canopy trees can touch, or can overshadow a proportion of the ground ranging down to 50%, determining the extent to which the grass layer can develop. There are some evergreens, but the trees are mainly deciduous and always produce a marked flush of shoot growth and new leaves at the end of the dry season. Many trees also flower at this time. Excavation of tree root systems showed well-developed tap roots of the order of two metres length, as well as an extensive system of laterals in the top 0.5 m; on one ridge-top site a tap root was traced down to 4.5 m. This new growth and flowering occurs before the new rains, apparently drawing on reserves of soil moisture left from the previous season's rains, and it is suggested that it is triggered by the rise of nocturnal minimum temperatures to growing season levels. Most grass roots, on the other hand, were found in the top 0.5 m only of soil, and in most cases grass growth did not begin until the rains started (Jeffers & Boaler, 1966).

Shifting cultivation is widely practised in *miombo* areas. Trees are felled and the debris burned during the dry season. Crops can then be grown for three to five years, until the nutrients from the burned vegetation are used up, when cultivation is abandoned. In the first few years after cessation of cultivation, grasses dominate, and fires are fiercer than before, but after 10-20 years the competition of woody species becomes more intense, and the canopy and understorey species begin to reassert their dominance (Boaler & Sciwale, 1966).

Based on the results of the *miombo* burning trials reported above, together with his own extensive observations in northern Zambia, Lawton (1978) suggested the following successional relationships:

- *mateshi*, a dry evergreen forest with a closed canopy up to 25 m high, a well-developed evergreen shrub layer and climbers, but a sparse ground layer, may be the original climax vegetation, but is currently reduced to scattered remnants. Most of the dominant species are fire-sensitive. This type of forest does not naturally produce enough grass to fuel bush fire;
- *chipya* is derived from *mateshi* by opening up the canopy for cultivation and by dry season burning. It consists mainly of perennial grasses, forbs and bracken (*Pteridium aquilinum*), but contains scattered small trees and small patches of low canopy. The characteristic species are fire-hardy and intolerant of shade, and the vegetation is subject to intense dry-season fires;
- the *Uapaca* genus includes a number of moderately fire-tolerant medium sized trees (usually >10 m). They are unable to survive among the grasses of the *chipya*, but



can invade the patches of canopy, where fire is less intense, and in their turn they provide increased protection from fire. This enables the dominant species of *miombo* woodland, *Brachystegia* and *Julbernardia* species, to grow through the sapling stage and form mature trees;

- *miombo* woodland has various possible outcomes, as described by Trapnell above. If protected from fire, it can revert to *mateshi*, but only in the higher rainfall areas (Hogberg & Pearce, 1986).

Hogberg and Pearce (1986) draw attention to the mycorrhizal implications of this successional pattern. *Chipya* is basically an AM community of grasses and scattered trees. Of the canopy trees, only one is possibly EM. Yet EM *Uapaca* spp. are able to get a foothold in the small patches of canopy and create conditions of partial fire protection (and EM network?) which allow the establishment and growth of the *Brachystegia-Julbernardia* group of EM species which become the dominants in the evolving mixed EM-AM *miombo* woodland.

#### **1.1.2.3. Human adaptations of savanna**

Shifting agriculture has been traditional in many savanna regions, small areas being partially cleared and planted. Trees which yielded valuable fruits or forage were left, and the others would be cut down for firewood but the roots often left and allowed to re-sprout or produce suckers. When available nutrients became exhausted the area would be left fallow for a long period, and the shrubs and trees would re-grow.

Rotational woodlots are a development of this traditional approach which has been successfully demonstrated in a de-forested region of NW Tanzania (Otsyina *et al*, 1996). Fast-growing tree species suitable for firewood and pole production are planted, and crops can be grown around them until the trees become too competitive for water, light and nutrients. Cropping is then discontinued, though light grazing is still be possible. This corresponds to the fallow phase in shifting agriculture. When the tree crop is ready for harvesting the area is clear-cut, but tree roots and stumps are left to re-grow. Soil fertility will have been restored, and crops can be sown again.

Farmed parklands are an alternative form of agroforestry. Valued species of trees, yielding fruit, nuts or forage, are permanent but normally isolated features, and permanent agriculture is pursued around and between them. In some cases there is a trade-off between the value of the trees' products and their competitiveness with the annual crops, but in other cases competition seems, surprisingly, to be negligible or absent (cf. the profiles of *Azadiracta indica*, *Parkia* spp. and *Vitellaria paradoxa* in Section 5.2).

There are a number of factors which make trees and herbaceous vegetation or crops less competitive and more complementary in the hot dry tropics than they could be in temperate climates: very long taproots, reverse phenology, hydraulic lift, the important shelter effect of trees against strong desiccating winds, and the shading which reduces the fierce soil surface temperatures prevalent in regions such as the Sahel.

## 1.2. Discussion

The demarcation of arid and semi-arid regions is shown in Figures 1, 2 and 3, and serves to define the main areas of interest in this study. Semi-arid areas receive, on average, enough rainfall to produce useful amounts of food, fodder or fuel, and many of them have traditionally supported substantial nomadic or settled populations. These areas are currently under great degradative pressure, and there is considerable scope and urgent need for soundly based and economically viable conservation and development. The more extreme arid areas can furnish useful information on plant survival strategies and on the functioning of mycorrhizal symbiosis in particularly harsh conditions, but are not likely to warrant reclamation measures. Predicted long-term trends in annual rainfall also need to be borne in mind; development measures appropriate in a stable climatic situation might not be viable if a gradual decrease in annual precipitation is anticipated.

Mediterranean ecosystems and tropical savanna have much in common. Both are adapted to long seasonal periods of water deficiency and to a considerable degree of variability. Both appear to be ancient ecosystems, but to have been greatly extended by human impact. They are transitional, and have been responsive to climatic fluctuations. They are both naturally subject to wildfire, and in many areas fire has regularly been used by man as a management tool since prehistoric times. Californian chaparral is an example of a natural fire climax ecosystem, and AMF and other symbiotic microbes appear to have adapted to vegetation which passes through a long-term cycle in which particular plant species recur regularly at a given stage of the cycle, but are present only in the soil seed bank for long periods.

Deep-rooting trees and shrubs, 'fertile islands' and a shading effect of the tree canopy beneficial to the herbaceous layer are shared features, and the cork oak/grass pasture areas of E Portugal and W Spain are examples of productive savanna-type land use towards the moister end of the mediterranean rainfall gradient.

The severe climatic stresses to which both types of ecosystem are subjected, together with the many shared features, suggest that mycorrhizal insights acquired from studies in one may well be valid for the other, and this could be very important in view of the sketchy state of mycorrhizal knowledge.

The resilience of tropical savanna in the face of harsh and unpredictable climatic stresses, together with the apparently harmonious coexistence of trees and grasses, suggests that anti-desertification strategies, whether defensive or aimed at the recovery of degraded dryland, should be based on supporting or re-establishing ecosystems or land-use systems in which trees and herbaceous vegetation or annual crops complement one another. Agroforestry rather than treeless agriculture or pure forestry may be indicated, with hedges, clumps or scattered trees providing shade, shelter from desiccating winds, and reservoirs of soil microorganisms, and in some cases producing leaves and fruits in the dry season, drawing on deep water. It seems possible that such a scattering of deep-rooting trees may draw on deep water sustainably, whereas an attempt to grow a forest of them might gradually deplete deep water resources. The ground-cover vegetation or crops minimize runoff and evaporation in the rainy season and sustain populations of soil fungi and bacteria, leguminous crop plants and trees playing a key part in replenishing soil nitrogen

levels. Ambiguity surrounds the role and impact of bushfire, but recycling vegetation through stall-fed livestock or by returning crop residues to the soil, thus enhancing soil organic matter, might be expected to support higher levels of soil microorganisms and plant productivity than the traditional use of fire.

Tree planting programmes may need to include firebreaks. In the Sahel they will also be designed to provide maximum shelter from desiccating Saharan winds. In a rolling topography in medium latitudes aspect can be crucial, slopes tilted towards the sun are likely to be a harsher outplanting environment than their opposites.

## 2. Desertification

The United Nations Conference on Desertification (UNCOD), held in 1977, defined desertification as "a reduction in the land production potential in arid, semi-arid and dry sub-humid zones, that may ultimately lead to desert-like conditions" (Hutchinson, 1996). The Earth Summit at Rio de Janeiro in 1992 attributed the problem to various factors, including climate variation and human activities (Le Houérou, 1996), and over-exploitation by man of fragile ecosystems has increasingly been seen as the key factor. The result is often a dysfunctional system involving a reduction of the mean residence time for resources entering the ecosystem or being produced by it (water, nutrients), (de Soyza *et al*, 1998).

### 2.1. The phenomenon

Desertification became an environmental issue of major concern in the 1970s. From the late 1960s the countries of the Sahel suffered severe and prolonged drought (Hutchinson, 1996). In a period of 25 years, annual rainfall virtually never reached the 1931-1960 mean (Le Houérou, 1996). This climatic disaster coincided with a period of population growth and consequent greater human pressure on natural resources. The resulting degradation of rangeland and areas of marginal rain-fed farming was particularly apparent in regions bordering on the Sahara, giving rise to fears that the desert was moving inexorably and irreversibly south, taking over areas that had previously supported substantial human populations (Hutchinson, 1996). Findings of a study in 1975 were extrapolated to give an annual rate of desert advance into the Sahel of 5.5 km a year (Thomas, 1997).

The desert advance theory has not gone unchallenged. Thomas (1997) has pointed out that the study that gave credence to it was in fact a comparison of wet year conditions in 1958 with very dry conditions in 1975. Satellite images showed the area of the Sahara steadily expanding from 1980 to 1984. But from then on there was a fluctuating but marked decrease in the area of the Sahara (Hutchinson, 1996). Dendrochronological studies, pollen analysis and lake level surveys suggest that long droughts comparable to the recent one have occurred in this region on several occasions within the last 2000 years, as well as in prehistorical and geological times. Tree-ring studies in the Atlas mountains of Morocco show that dry periods lasting 20 to 50 years occurred on at least 6 occasions between A.D. 1100 and 1850, and there are similar results from Algeria and Israel (Le Houérou, 1996). Arid and semi-arid ecosystems are adapted not only to low rainfall but also to a very high degree of variability, and left to themselves they display a high degree of resilience to drought. Le Houérou (1996) stresses that drought affects production but not long-term productivity, and cites examples of state-owned ranches in several Sahelian countries, protected and lightly stocked in accordance with their estimated long-term carrying capacity, that survived 25 years of drought without showing signs of desertification. Sullivan (1999) produces evidence that in N W Namibia communal pastoralism is not causing desertification, as is widely believed. However, though naturally resilient, dryland systems are fragile, as shown by some 30-year-old experimental exclosures in the Sahel where vegetation recovery has not occurred after drought, probably due to the impact of earlier insidious desertification processes on the soil's ability to support vegetation recovery (Thomas, 1997, citing an earlier study by Le Houérou). It has also been pointed out that revegetation of perennial grassland after heavy grazing pressure during drought may be

with scrub or other vegetation of less economic value (Hutchinson, 1996; Dougill *et al*, 1999).

Recent study has certainly led to some qualification of earlier, possibly simplistic presentations of desertification, but it has also shown how widespread this damaging process is, and that it is not new. Several desertification episodes can be pinpointed as contributing to current conditions in the Iberian peninsula. Archeological evidence is adduced for the claim that some badlands there were already in that condition 5000 years ago, due to human impact (Puigdefábregas & Mendizabal, 1998). In more recent times, extensive land-use changes occurred in the 16<sup>th</sup> and 17<sup>th</sup> centuries, driven by political and economic change but possibly encouraged by the slightly moister and cooler peak of a long-term climatic fluctuation; a southward expansion of dryland agriculture together with high demand for wool and wood products left large areas exposed to erosion, as shown by increased sedimentation rates in river deltas and by archeological and ecological evidence. A further damaging impact occurred in the first half of the 20<sup>th</sup> century, this time coinciding with a 50-year period during which rainfall not only decreased by an average of about 3 mm a year in SE Spain but became increasingly variable. Rural overpopulation led to the encroachment of agriculture on to rangelands and the increase of stock density, followed by grassland exhaustion and soil erosion (Puigdefábregas & Mendizabal, 1998).

Similar instances of desertification of vulnerable arid or semi-arid lands have been documented for the south-western USA (Fredrickson *et al*, 1998; Hutchinson, 1996), the Sudan (Ayoub, 1998), Jordan (Khresat *et al*, 1998), India (Ram *et al*, 1999; Singh, 1998),



China (Renzhong & Ripley, 1997; Zha & Gao, 1997; Mitchell *et al*, 1998), Crete (Hill *et al*, 1998), Argentina (Ojeda *et al*, 1998; Guevara *et al*, 1999; Busso, 1997) and the Maghreb (Puigdefábregas & Mendizabal, 1998). Reviewing the findings of several large and detailed studies covering central Asia, NW China, North Africa and the Sahel, based on a combination of remote sensing and detailed ground control, Le Houérou (1996) reports close agreement around a figure of 0.5 to 0.7% as the annual rate of desertification of these arid zones between the 1960s and 1980s.

## **2.2. The process**

The main causes of desertification are overgrazing and overstocking of rangeland, inappropriate cultivation, and deforestation or excessive wood harvesting. Drastic reduction or destruction of the perennial plant cover leaves the soil surface unprotected, and subject to erosion by water and wind (Le Houérou, 1996), (the Sahel, NW China, Mongolia and Patagonia experience strong and persistent wind regimes throughout the long dry season). Under extreme desertification conditions, soil erosion rates of 200-300 tonnes per hectare per year have been reported from several countries (Le Houérou, 1996). It is, of course, the topsoil, containing most nutrients and the macro- and microfaunas and floras, that is being blown or washed away. Bare surfaces become hard due to trampling by animals and crusting by raindrop splash, and rainwater is increasingly lost to potentially damaging runoff instead of infiltrating. Reduced plant cover means decreased production of litter and reduction in the organic content of the soil, and this results in lower biological activity from soil organisms, particularly symbionts, and a degradation cascade is set in motion (Le Houérou, 1996).

An example of this cascade can be seen in the extensive steppes of the western Mediterranean zone. These areas have annual rainfall ranging from 400 mm to 100 mm, and P/PET ratios between 0.25 and 0.05, and are mainly dominated by alfa grass (*Stipa tenacissima*) or plant communities associated with it. In the past, arboreal steppes of alfa mixed with open woods and shrubs were widespread. Most of this is long since gone in SE Spain. In the Maghreb, a population increase of 300% since 1950 has put enormous pressure on fragile natural resources. Excessive firewood harvesting is rapidly converting the arboreal steppe into a grass steppe. Only 6% of its area 50 years ago remains, and its primary production has declined to 40-20% of its value 50 years ago. Overexploitation of the grass steppe by grazing and harvesting of plant material has led to encroachment by steppic shrubs, a process which may eliminate the alpha grass. Puigdefàbregas & Mendizabal (1998) state that alpha grass can regenerate vegetatively but not by seed in the absence of shade. In comparison with grass steppes, shrub steppes have lost soil organic matter, and in intershrub areas they often develop physical or biological crusts that increase runoff at the expense of infiltration. Shrub steppes may be further degraded by water or wind erosion, depending on site characteristics. Some of these changes are considered reversible, but the decline from grass steppe to shrub steppe is generally seen as irreversible (Puigdefàbregas & Mendizabal, 1998).

### 2.3. Discussion

Historical evidence of the resilience of sub-Saharan regions in the face of several prolonged droughts is encouraging, and instances of recovery from serious but fairly recent environmental degradation in E Africa, reported in Sections 4.1 and 4.2., also offer grounds for optimism. However, the accumulated evidence of aggressive desertification from almost every continent, together with the pressure of increasing populations in several of the worst affected areas mean that soundly based defensive and recovery strategies are essential.

To people trying to gain a livelihood from their land desertification means a catastrophic drop in the productivity of their land. Appropriately used savanna or sustainable farming systems optimize the productive capacity of vulnerable dryland by absorbing and using water when it is available and by deploying effective survival strategies during drought. In contrast, desertified ecosystems are dysfunctional in that the primary limiting factor is not simply water but the system's impaired ability to retain and use water; instead of being absorbed and used productively by plants, animals and complex networks of soil organisms, much of the rainfall is rapidly lost through evaporation or potentially destructive runoff.

Healthy savanna has an inherent resilience, but overgrazing, excessive wood harvesting and inappropriate cultivation attack both the ground cover and the shelter, which exposes the soil to wind and water erosion, and deprives soil microorganisms of their carbon source. A characteristic degradational sequence in Mediterranean areas has been defined as arboreal

steppe to grass steppe to shrub steppe, each stage representing a loss in keystone plant species, in overall productivity and in usefulness to the human population. The concepts of keystone species and irreversible change are discussed in Section 4.3.1., where a keystone species is seen as a species with an essential role in a particular ecosystem, the loss of which takes the ecosystem to a lower level. Evidence from Spain, also discussed later, suggests that depletion of symbiotic soil microorganisms may be an important factor in this degradational cascade.

### 3. Mycorrhizas

After outlining the nature and distribution of the two main types of mycorrhiza, this chapter will note some important interactions with other soil microorganisms. Of these, the crucial plant-AMF-*Rhizobium* association has attracted much attention, but other possibly important interactions appear to have received little notice.

Most plants form mycorrhizas in natural ecosystems. Mycorrhizas impose a cost on the plant but can bring nutritional and other benefits, and it seems likely that these are particularly important in drought-stressed ecosystems. Studies in Namibia suggest that the plants and their fungal partners are very closely attuned to each other in their responses to rain and drought. For some dryland perennials, the exploitation of deep soil resources is a key strategy, and there is evidence of plant-microbe coordination around deep water-tables. In experimental conditions, some plant species exhibit a high degree of mycorrhizal dependency, whereas others do not, but the legumes and C<sub>4</sub> grasses which are among the most characteristic and valuable semi-arid plant species tend to be coarse-rooted and therefore more mycorrhiza-dependent. In the light of these facts, it would be surprising if these plants were able to thrive in desertified, mycorrhiza-deficient soils.

#### 3.1. Arbuscular mycorrhizas

Arbuscular mycorrhizas are symbioses formed by members of the fungal genera *Glomus*, *Sclerocystis*, *Acaulospora*, *Entospora*, *Gigaspora* and *Scutellospora* (of the order Glomales, phylum Zygomycota) in the roots of an enormously wide variety of host plants

(Smith & Read, 1997). These fungi are thought to be obligately asexual, but to have evolved into recognizable and quite diverse taxonomic groups by mutation. About 150 species-level taxa have been described. These are not species in the normal sense of interbreeding groupings, but have been called 'form-species' (Smith & Read, 1997).

There can be considerable variation within a given AM fungal species. A possible genetic mechanism is discussed in Bever and Morton (1999) and in Giovannetti *et al* (1999). In a comparative study of three isolates of *Glomus mosseae* from dissimilar habitats, in which the fungus was grown with *Melilotus officinalis* in a range of different soils, moisture and temperature regimes, Stahl and Christensen (1991) showed that the three isolates varied significantly in their responses to the different environmental factors, and in their effectiveness as symbionts. AM fungi can adjust to low and high levels of soil nutrients, forming locally adapted strains, and local isolates have been found most effective in increasing plant yield (Lambert *et al*, 1980; Haas & Krikun, 1985; Gianinazzi-Pearson *et al*, 1985). Boerner (1990) found isolates of *Glomus ocutum* from infertile sites produced more biomass in *Geranium robertianum* than isolates from fertile sites.

The spores are very large, long-term survival structures. Infected root fragments also act as propagules (Tommerup & Abbott, 1981). Spores of some species are initially dormant, but after storage become quiescent but capable of rapid germination under appropriate conditions of moisture and temperature (Tommerup, 1983). Daniels and Trappe (1980) pointed out that the optimum temperature, pH and moisture conditions for germination of the AM fungus they were studying are those most suitable for the growth of a variety of

potential host plants. Young roots are readily colonized, but older roots may be less susceptible (Brundett *et al*, 1985; Brundett & Kendrick, 1990). The study by Brundett *et al* shows how rapid AM formation and development can be in optimum conditions. When 3-week leek seedlings were transplanted to positions around the base of an established *Glomus versiforme*-leek pot culture, penetration points were found on seedling roots by day 2, and by day 6 approximately 40%, 20% and 6% of the root length contained internal hyphae, arbuscules and vesicles respectively.

Low numbers of propagules (e.g in eroded sites) may result in low levels of colonization, so it is necessary to evaluate the infectivity or propagule density in soil, in order to predict outcomes of restoration programmes or growth of crops (Reeves *et al*, 1979; Allen, 1989).

Undisturbed hyphal networks can survive and retain infectivity during periods when the vegetation on which it developed is dormant or dead, and can rapidly colonize when favourable conditions return (McGee 1989; Jasper 1992; Jasper *et al* 1989, 1991, 1993; Braunberger *et al*, 1994).

Between 4-20 % of net photosynthate is transferred to the fungus and used in the production of vegetative and reproductive structures, and in respiration (Johnson *et al*, 1997). In return, the fungal mycelium proliferates through the soil, taking in mineral nutrients which are then shared with the plant.

Nutritional benefits are not the only advantages accruing to the plant from the association;

mycorrhizas can contribute to plant fitness by protecting it from pathogens (Smith & Read, 1997, citing Newsham *et al*, 1995). They may increase water uptake (Allen, 1982), but Bryla and Duniway (1997a,b) offer contrary evidence. Koide and associates reported not only enhanced growth of mycorrhizal plants but also enhanced reproductive performance (more and larger seeds with higher P content, and greater offspring vigour) (Lewis and Koide, 1990; Stanley, Koide & Shumway, 1993; Sanders & Koide, 1994; Heppell, Shumway & Koide, 1998). Roldán-Fajardo (1994) reported a 63% increase in the number of seedlings around a mycorrhizal grass that had shown no growth response to AM inoculation.

### 3.2. Ectomycorrhizas

The number of fungal species forming ectomycorrhizas is much higher than for AMs. Smith and Read (1997) report estimates of 5000 to 6000 species by Molina *et al* (1992), and it is thought that the majority but not all of ectomycorrhizal fungi have a broad host range. Some of the most widely occurring EM fungal species have a high degree of intraspecific variability (Smith & Read, 1997). In a study of intraspecific diversity of *Hebeloma cylindrosporum* on *Pinus pinaster*, samples were taken from 14 stands located along a 150 km stretch of the French Atlantic coastline, and it was found that local populations could be almost as genetically diverse as the entire population of these widely separated stands (Guidot *et al*, 1999). The fungi known to be involved in ectomycorrhiza formation are largely basidiomycetous, but the list also includes some Ascomycota and others (Wilcox, 1996). Harley and Smith (1983) listed 45 genera of Basidiomycota and 18 genera of Ascomycota as including one or more species reported as ectomycorrhizal (cited



by Wilcox, 1996).

Extraradical hyphae from ectomycorrhizas extend from the mantle into the surrounding soil, scavenging for nutrients over distances up to several metres, a much greater distance than AMF hyphae can reach (Marschner & Dell, 1994).

Ectomycorrhizas on a particular root normally involve a single fungal species. Successional replacement by different fungal species has been observed as the tree matures. (Mason *et al*, 1983). Where this occurs, it is likely to be when roots resume growth after periods of dormancy. Late-stage fungi appear to be unable to form mycorrhizas on young seedlings except in axenic conditions or when the young seedlings germinate under the canopy of a mature tree of the same species. It may be that a late-stage fungus requires better access to C than a young seedling on its own can provide (Gibson & Deacon, 1990), and that where it does successfully colonize a seedling it is being sustained by C from the established tree from which the colonizing hypha originated. The so-called early-stage type would find its niche in pioneer situations or in tree nurseries (Smith & Read, 1997).

Many ecosystems dominated by ectomycorrhizal plants are characterized by low availability of N, and it has been increasingly recognized that some ectomycorrhizal fungi have access to N which is in organic combination in decomposing litter in the superficial layer of soil occupied by ectomycorrhizal roots (Smith & Read, 1997).

A number of studies have shown that ectomycorrhizal colonization significantly increases P

inflow into the plant, and the role of the extraradical mycelium in exploring the soil and facilitating the mobilization of P from complex inorganic and organic sources has been emphasized. Experiments with *Pinus radiata* suggest that mycorrhizal roots not only take up P and transfer it steadily to the plant but also accumulate and store it in the fungal sheath and transfer it from there to the plant when the flow of P from the soil ceases and the plant still needs it (Morrison, 1962; Smith & Read, 1997).

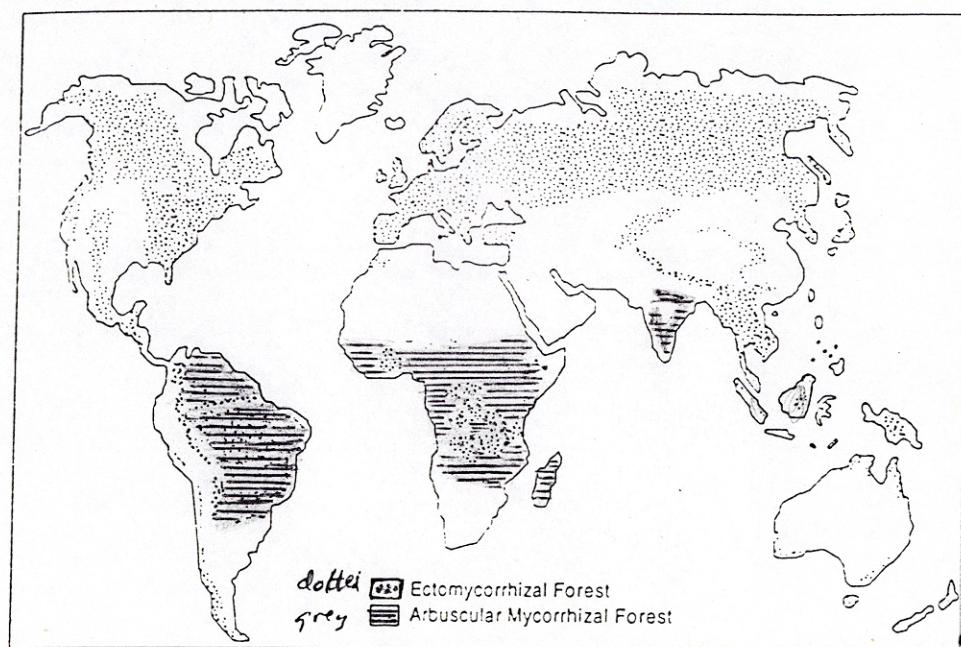
### 3.3. Distribution of the major types of mycorrhiza

A few families of plants, notably Brassicaceae, Amaranthaceae and Caryophyllaceae, are characteristically non-mycorrhizal. The majority of species in this category are ruderals of disturbed habitats, and are excluded from most closed plant communities (Francis and Read, 1994).

However, mycorrhizal symbioses are otherwise nearly universal in terrestrial plants, about four fifths of which are thought to form endomycorrhizas (AM). These include most herbaceous plants that have been studied (Smith and Read, 1997). They dominate arid and semiarid biomes (including cold deserts as well as hot deserts and semi-deserts), strands and dunes, temperate grasslands, and much savanna (Allen *et al*, 1995; Brundett, 1991; Bethlenfalvay *et al*, 1984; Koske, 1975). Many tree species of great economic value are AM hosts; the list includes *Citrus*, *Coffea*, *Cacao*, *Vitis*, *Malus* (apple), *Prunus* (peach), *Persea* (avocado), *Elaeis*, (oil palm), *Anacardium* (cashew) and most tropical hardwoods (Smith & Read, 1997). Ectomycorrhizal (EM) host plants are nearly all woody perennials.(Smith & Read, 1997). They include the Pinaceae, some Cupressaceae,

Fagaceae, Betulaceae, Salicaceae and Dipterocarpaceae, and most Myrtaceae and Caesalpinioideae (Family Fabaceae), (Malloch *et al*, 1980; Newman & Redell, 1988), and provide the dominant trees in vast areas of boreal and temperate forest.

Allen *et al*, (1995), print a map of the distribution patterns of AM and EM forests worldwide, modified from Moser (1967), shown below as Figure 5.



**Figure 5.** Distribution of AM and EM forests of the world.

There are three factors which help to explain this distribution pattern:

(a) *The latitude/altitude gradient*; EM become increasingly prevalent at higher, but not extreme, latitudes or altitudes, (Moser, 1967; Smith & Read, 1997).

(b) *The soil organic matter gradient*; AM fungi tend to be more abundant in (mineral) soils of low organic matter, while EM fungi generally occur in soils with higher surface organic matter (Allen *et al*, 1995; Francis and Read, 1994).

(c) *Evolutionary history*; it is thought that landplants and *Glomus*-like (AM) fungi may have co-evolved from about 415 million years B.P., and that Pinaceae and the ancestors of EM fungi co-evolved from about 130 millions years B.P. (Smith and Read, 1997). Malloch *et al* (1980) believe that now-dominant EM forests may often have expanded at the expense of endomycorrhizal forests, and that they must have a selective advantage in many extreme environments, though not the most severe arid climates (at high elevations, in strongly seasonal climates, on very poor soils, and possibly in the adaptation of certain pines to seasonal burning). They give as an example the AM trees and shrubs that formed mixed forests over much of N.America earlier in the Tertiary, but became extinct over most of the area following increasing aridity in the mid Pliocene and have been replaced by extensive EM forest.

Constraints on plant growth imposed by low availability of N are a characteristic of many ecosystems dominated by EM plants (Smith & Read, 1997). Malloch *et al* (1980) suggested that ectomycorrhizas may have the ability to absorb and utilize organic nitrogen

taken directly from decaying organic matter, whereas endomycorrhizas may lack the necessary enzymes. Smith & Read (1997) quote evidence to support this, pointing out that ectomycorrhizas develop in the upper organic layers of the soil or in the interface of organic and mineral layers and that roots proliferate preferentially in the fermentation horizon (immediately below the freshly fallen surface litter layer), the most important site of N mobilization. Their Table 15.1 lists extracellular enzymes produced by ectomycorrhizal fungi that may provide access to N and P by attacking the structural components of litter. This apparent ability to acquire nitrogen before it is converted to a form available to AM fungi would confer a powerful advantage on EM competitors in N-limited situations.

Situations where P is the primary limiting factor, on the other hand, appear to favour the prevalence of AMF colonization (Smith & Read, 1997). However, large-scale studies in Korup National Park, located in lowland Cameroon rainforest, revealed a considerable presence of EM trees in a situation where soils were in general low in P, and where overwhelming AM dominance might have been expected (Newbery *et al*, 1988). Twenty three species were found to be ectomycorrhizal; they tended to be grouped in clumps or groves, growing in forest otherwise composed of AM trees. A striking feature was the extent to which the accumulated organic matter in these groves was colonized by ectomycorrhizal roots and hyphal strands. The authors cite mounting evidence that some ectomycorrhizal fungi have access to organic sources of both N and P, and suggest that local dominance of EM over AM trees may be due to an ability to utilize organic P, thus preventing potentially mineralizable phosphorus from entering the soil pool. The EM



fungal sheath would offer additional advantage, being capable of storing phosphorus made available by seasonal pulses of organic matter input.

The EM species featuring in the Korup study were almost all Caesalpinoideae, a group of mainly non-nodulating legumes which includes many EM species, some AM species and a few species with both types of mycorrhiza. EM Caesalpinoids also provide the dominants in the miombo woodlands which occupy large semiarid areas of central Africa. The possible ability of their fungal partners to utilize organic N and P could explain the competitive advantage apparently enjoyed by these trees in this region. There are no long-term demographical data from Korup to show whether the EM groves are contained by limiting factors locally or whether they will expand until they coalesce to give a uniform cover of EM species (Newbery *et al*, 1988), but there is some evidence of miombo woodland succession which was examined in Section 1.1.2.2.

The sub-family Caesalpinoideae (Fabaceae) includes species of wide distribution and economic value, including the genus *Cassia*, with many species in Africa and N.America, and the carob, *Ceratonia siliqua*, widely distributed around the Mediterranean basin and traditionally cherished by peasant farmers. The carob might repay study in the context of efforts to improve vegetation on marginal semiarid land.

Hogberg (1986) suggested that in tropical Africa ectomycorrhizal legumes are most abundant in closed forest or woodland on soils low in phosphorus, with a closed nitrogen cycle, while nitrogen fixing, AM legumes become more abundant towards drier areas,

simultaneous with an increase in soil phosphorus and a decline in nitrogen (cited by Newbery *et al*, 1988).

An interesting insight into AM/EM competition arises in observations reported by Kovacik *et al*, (1984). An established EM *Pinus ponderosa* forest in Colorado suffered beetle kill of the dominant pines over large areas. This provided an opening for the rapid invasion of previously absent AM plants and inoculum (the understorey had previously consisted mainly of non-mycorrhizal sun sedge). It is thought that live pines may deploy allelopathic deterrents to AM host plants.

A fundamental difference between AM and EM systems is that AM networks tend to promote species-rich plant communities (Grime *et al*, 1987), while EM networks promote dominance by a few species (Newbery *et al*, 1988). This is because there are very large numbers of plant species susceptible to AM infection by a small number of fungal species, and host-fungus specificity is absent or low (Smith & Read, 1997), while with the ectomycorrhizal relationship, the reverse is the case, upwards of 5000 fungal species are involved, while only a small number of plant species are susceptible to this type of infection. The majority of EM fungi have a broad host range, but a degree of specificity can also be recognized (Smith & Read, 1997, who cite studies showing that *Eucalyptus*, *Nothofagus* and *Pseudotsuga* each have an extensive assemblage of specific fungi). Thus, AM forests will have a wide range of tree and other species, while EM forests will be dominated by a few related tree species, or even be monospecific.

In a semiarid *Eucalyptus*-dominated open scrub community in S.Australia, McGee (1986) found many species with both EM and AM infection, with annuals having both for the whole growing season and perennials usually exhibiting either a predominantly AM or EM association. *Eucalyptus* species themselves can form both types of mycorrhiza (Brundett and Abbott, 1991; Jones *et al*, 1998), and Lapeyrie and Chilvers (1985) observed a succession, in which early infection was almost entirely by AM fungi, with ectomycorrhizas forming later and tending to replace the endomycorrhizas. This sequence was sometimes evident on a single root, with the EM fungus occupying the most recently formed (root tip) region. The same succession appears to occur in *Uapaca kirkiana* (cf. Section 5.3).

In a succession of dune ecosystems (calcareous-acidic and dry-wet) in Holland, both EM and AM colonization of *Salix repens* was observed. Fluctuations between the two types appeared to be seasonal rather than successional (van der Heijden & Vosatka, 1999).

### **3.4. Interactions between mycorrhizal fungi and other soil microorganisms**

Mycorrhizal fungi and plant roots operate their symbioses within the context of a complex web comprising a variety of soil animals and microbiota, and a range of competitive or mutualistic relationships with these other organisms affect the plant-fungus interaction. A few of these relationships have been studied, but many are unknown.

Mycorrhizal fungi and soil bacteria can function synergistically in a number of ways. Germination of AM fungal spores can be increased in the presence of certain soil bacteria



(Azcón, 1987; Mayo *et al*, 1986; Fitter & Garbaye, 1994), and Garbaye proposed the term 'mycorrhization helper bacteria' for bacteria which consistently promote mycorrhizal development. He reviewed evidence for bacterial involvement in the early, free-living stage of the fungus' development, including studies of the enhancing effect of fluorescent pseudomonads on mycorrhiza establishment between Douglas fir and the ectomycorrhizal fungus *Laccaria laccata* Scop. ex. Fr. (Duponnois & Garbaye, 1989; Garbaye, 1994; Frey-Klett *et al*, 1997, 1999; Barea *et al*, 1998; Budi *et al*, 1999). Bianciotto and co-workers (1996) detected a bacterial symbiont, identified as a pseudomonad, within the cytoplasm of spores and mycelium of *Gigaspora margarita*. They could not explain its functional significance, but suggested that these bacteria are a stable component of the fungal cytoplasm.

It has been shown that phosphate-solubilizing bacteria can hydrolyze insoluble phosphate, including rock phosphate, *in vitro*, and researchers using a low-phosphate alkaline soil amended with a range of concentrations of rock phosphate reported that plants inoculated with both AMF propagules and phosphate-solubilizing bacteria took up more P than plants with only one or neither of these inocula (Azcón *et al*, 1976; Toro, Azcón & Barea, 1997).

There are important interactions between mycorrhizal fungi and nitrogen-fixing nodulating bacteria, particularly in low P soils. Both *Rhizobium*- (and *Bradyrhizobium*-) and *Frankia*-associated plant species are normally mycorrhizal, and the mycorrhizal and nodulating symbioses typically act synergistically, both on infection rate and on mineral nutrition and growth of the plant (Fitter and Garbaye, 1994; Manjunath *et al*, 1984; De la Cruz *et al*,

1988). Mycorrhizal fungi enhanced nodulation, shoot and root dry weight and levels of nitrogen, calcium and phosphorus in a dually inoculated actinorrhizal shrub (*Ceanothus velutinus*) (Rose and Youngberg, 1980); mycorrhizal inoculation alone produced only slight increases, *Frankia* inoculation alone produced large increases, but dual inoculation produced 3-fold increases over *Frankia* alone. Nodulating *Ceanothus* species are early colonizers in edaphically or climatically stressed sites (Rose and Youngberg, 1980; Rose, 1980) (cf. Section 1.1.1.3.). The mycorrhizal fungus not only colonized the plant roots but was also found within the nodules; however, the enhancement resulting from the dual infection is attributed to an improved nutrient status of the host rather than a direct interaction between fungus and bacterium (Rose and Youngberg, citing Daft and El Giahmi, 1976). The nitrogen fixation process has a high P requirement, and it appears that by increasing the supply of P to plant and nodule, the fungus enables greater fixation of nitrogen to be effected by the bacterium.

Similar interactions between AMF and rhizobium strains are well documented by many workers (Asimi *et al*, 1980; Olesniewicz & Thomas, 1999; Barea *et al*, 1987, 1997; Carpenter & Allen, 1988). Results show how specific the functional compatibility relationships between these symbionts are; certain combinations of appropriate AMF and local rhizobia were associated with strikingly enhanced plant growth and increased uptake of P, but a wide range of results were produced by the different combinations of microbial treatments tested, and some combinations were disadvantageous (Requena *et al*, 1997; Azcón *et al*, 1991). Work with chemically induced mutants of *Pisum sativa* showed an association between the *myc*- and *nod*- genes, suggesting that there is a genetic linkage in

the mechanisms controlling this host plant's response to mycorrhizal and rhizobial colonization (Graham & Eissenstat, 1994).

Plant-growth-promoting rhizobacteria (PGPRs), isolated from a representative area of a desertified semi-arid ecosystem in SE Spain were also included in the trials by Requena and associates. In single inoculation, PGPRs were found to have a positive effect on plant emergence and growth in non-sterile but not in sterile soil, suggesting a role in the biological control of plant pathogens. However, when used in combination with the other inoculants, a range of positive and negative effects on plant growth and shoot P content were observed. This important research is described in Section 4.3.3. The general conclusion from these trials in SE Spain was that in a land reclamation strategy using native woody legumes produced under non-sterile conditions, native AMF species and local isolates of rhizobia and PGPRs are most likely to be effective, and should be tested for functional compatibility in non-sterile soil of the target area.

The research reported in this section draws attention to the fact that the plant-AMF symbiosis does not operate in isolation. The compatibilities of legumes and various rhizobial or other nodulating bacteria have been widely investigated and are of fundamental importance. Effective combinations of plant + mycorrhizal fungus or plant + mycorrhizal fungus + *Rhizobium* etc should be the first objective, but testing these in non-sterile local soil may bring additional microbial factors into play, and it is necessary to be alert to this and to exploit it where possible.

### 3.5. The mycorrhizal ecology of drought-stressed ecosystems

Plants growing in a wide range of dryland sites have been shown to be AM. In a study conducted in the Red Desert of Wyoming (annual precipitation 150-200 mm, mostly occurring as snow), the majority of plants in undisturbed areas were found to be mycorrhizal, including shrubby *atriplexes* (Miller, 1979). A survey of perennials in a southern Californian area characterized as arid to extremely arid found all plants examined to be mycorrhizal (Bethlenfalvay *et al*, 1984). In a protected natural park area of the central dune field of the Namib desert, where grazing is limited to occasional small, nomadic herds of oryx and springbok, AM fungal communities were found to be an integral part of the ecosystem at sampling sites along two transects lying along a moisture gradient of <20 to 100 mm average annual rainfall, but with a highly variable pattern of localized storms (Jacobson, 1997).

Jacobson (1997) also studied micro-gradients of available moisture and of sand movement across the dune slopes at two of the Namib sites. Though *Glomus* species were found to be associated with grasses at all sites, not all plants were found to be mycorrhizal, and she concluded that the limits of tolerance for AM fungal communities were being revealed both at the driest (western) end of the moisture gradient, and on the exposed upper dune slopes of the eastern sites; in these places, plant roots were constantly exposed and reburied in the dry season, resulting in low retention of any spores produced. The only grass species to tolerate these conditions was *Stipagrostis sabulicola*, and it was only occasionally found to be mycorrhizal. The earlier work by Bethlenfalvay and others (1984) led them to infer that AMF associations are necessary for the survival and growth of plants in deserts; this

generalization clearly needs slight qualification, but is substantially supported by Jacobson's (1997) findings, and the implication is that if desertification has reduced the concentration of viable AMF propagules to inadequate levels, it will not be possible to re-establish useful plant communities without at the same time re-introducing their AMF partners.

The ubiquity of AM fungal communities in these undisturbed desert ecosystems implies that the fungal species involved are highly adapted to the harsh conditions arising from precipitation patterns which are low, seasonal and extremely variable. Jacobson (1997) reported a rapid and opportunistic growth response to the sporadic and unpredictable rain events. Four days after rain, germinating grass seedlings of facultatively annual species were visible but not mycorrhizal, but by 7 days mycorrhizal colonization was observed. Fungi and plants grew vegetatively as long as moisture was available; with declining moisture availability, seed-set ensued. The first observation of spore production corresponded with seed production by the plant, suggesting that plant and fungal phenologies could be linked. This suggestion was supported by the observation that isolates of the same fungal species growing with perennial plants with access to deep moisture continued growing through the dry season.

### 3.5.1. Vertical distribution of AM fungi

AMF mycelium and propagules have normally been found mainly in the topsoil. In a sagebrush steppe community in the semi-arid western USA, mycorrhizal infectivity was significantly reduced below 30 cm depth and approached zero at less than 1 m depth (Schwab & Reeves, 1981). But they can extend deep into the soil profile (Allen, M.F., 1991). Virginia *et al* (1986) found arbuscular mycorrhizas associated with *Prosopis* sp. concentrated up to 4 m deep in a sand desert in a nutrient-rich zone immediately above the water table, and Varma (1995) cites evidence from Neeraj (1992) that in arid areas in India mycorrhizas are commonly observed distributed throughout deep soils in *Prosopis* spp., with mycorrhizal hyphae tending to be most active near the water table, down to 4.6 m or even deeper.

This evidence of mycorrhizal activity at considerable depths, together with the deep-rooting strategies of key woody species (cf. Section 1.1.2.) suggests that attention should be given to the possible special significance of deepsoil processes in dryland ecosystems. Richter and Markewitz (1995) argued that the C horizon (the loose material deriving from the parent bedrock and lying between it and the B horizon or subsoil) should be included within the concept of soil, since not only chemical but also biological processes of soil formation occur there. In a *Pinus taeda* forest they found bacterial cells present in high numbers throughout the 8 m soil profile under study, and fungi also present though only in low concentrations in the deeper sectors.

Root nodules containing rhizobia were isolated from depths down to 7 m. at arid sites in New Mexico and California (Jenkins *et al*, 1988), and it was thought probable that deeply rooted legumes such as *Prosopis glandulosa* nodulate as deep as 10 m. The rhizobial populations were found to increase with depth, and to occur mainly well below the surface 0.5 m. of soil where the greatest root mass developed. This was taken to imply that the reported scarcity or absence of nodulation in shallow roots of woody legumes in drylands may be misleading; the symbiosis may have lapsed in the topsoil but be fully active deeper down. In the light of Neeraj's evidence (above) it seems possible that the same may be true for mycorrhizal symbiosis, so mature trees that no longer appear to be mycorrhizal near the surface may have carried symbiotic partners into deep root zones, where they may still be active and indeed crucial. This would clearly be difficult to confirm, but may have important practical implications, in that programmes for the mycorrhizal inoculation of trees with a deep-rooting strategy might benefit from the inclusion of AMF species adapted to deep soil conditions.

Confirmation of biological activity at great depth in dryland ecosystems is provided by Freckman and Virginia (1989), who found plant- (and hyphae-)feeding nematodes in the rhizosphere of *Prosopis glandulosa* at depths down to 12 m.

Two North American studies found a variety of AM fungal species active in the topsoil but only one species at deeper levels; M.F.Allen (1991) found four AM fungal species in the top 20 cm under *Artemisia tridentata*, but by 60 cm only *Glomus microcarpum* was left; in deep tallgrass prairie soil, five AM fungal species were found down to 100 cm, but only

one of them, *Glomus fasciculatum*, was found in all soil samples down to a depth of 220 cm (Zajicek *et al*, 1986).

These findings argue strongly in favour of a programme of research focussing on the inoculation of deep-rooting trees with AMF species known to function at great depth as well as near the surface. *Glomus fasciculatum* and *Gigaspora margarita* appear to be prime candidates, having been found at 34 m depth (cf. Section 5.4 ).

### 3.5.2. Mycorrhizal dependency

Apart from the special cases of species able to colonize unstable sand dunes, and ruderal species moving in quickly to exploit a temporary nutrient flush in a disturbed environment, plant communities appear to be increasingly dependent on mycorrhizal symbiosis along a gradient towards greater aridity and nutrient-poverty. Experiments in Panama found small-seeded pioneer tree species to be more dependent on mycorrhizal inoculation for initial survival and growth (Kiers *et al*, 2000); it seems possible that there might be a link between small-seededness and mycorrhizal dependency in dry ecosystems too.

M.F.Allen (1991) found arbuscular mycorrhizas extending downwards in cracks in shale and sandstone parent material to depths of 70 cm, and early studies of dwarf shrub communities growing in shallow calcareous soil on soft fissured rock in Israel suggested that shrubby species which thrive without mycorrhizas in more fertile soils were, in this habitat, dependent on mycorrhizas for nutrients (phosphorus and iron) which would otherwise have remained in an unavailable form due to the presence of excess calcium



carbonate (Litav, 1965). A pot experiment in southern Spain using calcareous soil of pH 7.6 with added rock phosphate suggested a possible synergistic effect of phosphate-solubilizing bacteria and particular AMF species on plant P uptake and growth in such situations. Control plants without either bacterial or AMF inoculum derived no benefit from the rock phosphate (Azcón *et al*, 1976).

The morphology of roots is an important factor in determining mycorrhizal dependency. Plants having coarse roots with little branching and few or no root hairs (magnolioid type) are more likely to show greater AMF colonization and positive growth response than those with fine, highly branching roots and many root hairs (graminoid type) (Smith & Smith, 1996, citing Baylis, 1975; Mason & Wilson, 1994). Experiments with characteristic grasses and forbs from North American tallgrass prairie found that the dominant warm season C<sub>4</sub> grasses were highly dependent on mycorrhizal inoculation, without which they did not grow and often died. The forbs (thought to be C<sub>3</sub>) were also fairly dependent. These two categories of plant are both coarse-rooted. In contrast, the cool season C<sub>3</sub> grasses with their graminoid root habit benefitted only moderately or even insignificantly from mycorrhizal inoculation (Hetrick *et al*, 1988).

Legumes also generally have a coarse root system. Nitrogen fixation by rhizobia is an energy-requiring process, so enhanced P uptake via AM fungi is particularly important (Sieverding, 1991). Habte & Manjunath (1987) found *Leucaena leucocephala* very highly dependent on AMF, and other fast-growing legumes are also reported to be dependent to lesser extents (Habte *et al*, 1993; Mason & Wilson, 1994, citing Habte & Turk, 1991).

Barnes (2001) reported that *Acacia erioloba* did not nodulate, but appeared to obtain most of its nitrogen from ground water; this may not be a unique feature and invites speculation as to the effect it may have on the mycorrhizal dependence of non-nodulating legumes. EM tropical Caesalpinoids are also non-nodulating and they too appear to have access to an alternative nitrogen source (Newbery *et al*, 1988). Could mycorrhizal dependency be primarily for an enhanced P supply in the case of nodulating legumes, but for alternative pathways of N acquisition in the case of non-nodulating legumes?

### 3.5.3. Survival strategies

Like plants, mycorrhizal fungi in seasonal or unpredictable climates need survival strategies to live through periods of environmental stress. EM fungi store and share considerable resources in dense networks and interconnected mats. AM fungi have much less storage capability, and go into dormancy. Their special dormant phase is the spore, but hyphal networks and living fungal structures within fragments of senescent or dead plant root can regenerate after varying periods of dormancy. Tommerup and Abbott (1981) observed hyphae resembling germ tubes of AM fungi emerging from mycorrhizal root fragments in soil that had been stored dry for up to 2 years. In experiments following up this observation they found that hyphae of *Glomus monosporus*, *Glomus fasciculatum* and *Gigaspora calospora* germinated from within dried root fragments after 6 months storage in dry soil at a matric potential of -50 MPa and colonized young seedlings, whereas hyphae of *Acaulospora laevis* and *Glomus caledonium* did not.

Two areas of mycorrhizal malfunction have attracted considerable attention, and may cast light on the natural survival mechanisms which have been compromised; long fallow disorder in cultivated land in Australia, and revegetation problems after disturbance by opencast mining and topsoil storage in USA.

#### **3.5.3.1. Evidence from Australia, Somalia and Spain**

Long fallow disorder is a phenomenon that has been observed in low P, cracking clay soils in Queensland and New South Wales. Normal agricultural practice there has been to cultivate fallow ground to control weeds and conserve moisture and nitrate for the next crop. A fallow period with bare soil will normally last about 6 months, but when changing from a winter to a summer crop, or when rains are insufficient, fallows of longer than 12 months can occur. Poor crop growth has been widespread in such circumstances. Crop species are all known AM hosts, and evidence has been produced that the disorder arises from a decline in viable AM propagules (Thompson, 1987, 1990, 1994). The implication was that a season without plant cover caused this decline, either because propagules were not adapted to dormancies exceeding one season or because the soil disturbance damaged them. Spores are robust structures, and their redistribution by cultivation should enhance rather than reduce the infectivity of the soil, but hyphal networks would be disrupted by mechanical disturbance of the soil, and fungal propagules within senescing or dead roots might well also be damaged.

However, in subsequent experiments with similar arable soils, neither intact soil cores nor soil samples that had been mechanically disturbed and then dry-stored for 18 months

showed reduced infectivity, whereas periodic wetting and drying of soil did have this effect, particularly when the soil had been disturbed. It was concluded that the factor responsible for the loss of infectivity of this land was rainfall occurring during the bare fallow and leading to untimely germination of fungal propagules in the absence of plant hosts (Pattinson & McGee, 1997).

Australian research suggests a variety of AMF survival strategies, depending on soil and climate types and also on differences between fungal genera (McGee, 1989). It is thought that in soil which is regularly cultivated and cropped, spores and root fragments are selected for as the main source of mycorrhizal infection at the beginning of the growing season, whereas in undisturbed soils supporting native vegetation, the hyphal network is more important (McGee *et al*, 1997). Cultivation is therefore likely to change the balance of AMF species present; this observation has been made in N America and Spain too (Hendrix *et al*, 1995; Requena *et al*, 1996). In a sandy area of open mallee scrub in South Australia, spores were scarce and showed delayed germination; early initiation of mycorrhizas appeared to be due to non-spore propagules, and it was suggested that spores might function as a reserve, should seasonal conditions kill fungi that had germinated with the first rains (McGee, 1989).

Evidence from Western Australia supports the view that in forest soils and other native perennial systems, spore numbers are low and infectivity depends heavily on infective roots and possibly on the presence of intact hyphal networks. In these circumstances, disturbance of the soil drastically reduced mycorrhizal colonization, even though there had

been no wetting of the soil during the dormant phase – the climate in this area is mediterranean (Jasper *et al*, 1989, 1991). Similar results were reported from Somalia, where bioassay found:

- 200 propagules/100 ml topsoil in *Terminalia brevis* forest,
- 60 propagules/100 ml topsoil in *Acacia nilotica* woodland,
- 35 propagules/100 ml topsoil in open degraded bushland with 8% plant cover,
- 0 propagules/100 ml topsoil in open degraded land with 3 % plant cover.

The open areas had been degraded by heavy grazing, logging and clearing for shifting agriculture. The authors caution that representative soil sampling is difficult in patchy degraded bushland, and it would be interesting to know the infectivity of soil in the rhizosphere of *Acacia nilotica* in the woodland that was sampled. But these reports highlight the crucial loss of mycorrhizal infectivity where such soils are disturbed or cleared (Michelsen & Rosendahl, 1989).

A study of abandoned marginal land in SE Spain found strong correlation between agricultural use and depletion of total organic carbon (TOC) and of AMF (shown by reduced spore counts and root infection percentages). Degradation continued for several years after abandonment and there was then a gradual recovery, with TOC and fungal propagule levels reaching values comparable to those in the undisturbed control after about 45 years (Roldán *et al*, 1997).

### 3.5.3.2. Evidence from the American West

U.S. legislation requires that topsoil is replaced over recontoured spoil after opencast coal extraction, and topsoil is frequently stored for several years before being replaced. Experiments in North Dakota found that topsoil stored in a 5 m deep pile for 3 years suffered a substantial reduction of mycorrhizal infectivity (when compared with undisturbed but otherwise comparable soil from nearby), and it appeared that the adverse effect was on root fragments rather than on spores (Rives *et al*, 1980). Gould and Liberta (1981) sampled the same sites 15 months later, and reported a further reduction in infectivity of the stored soil, though this might have been a seasonal difference.

No adverse effect on either mycorrhizal infectivity or plant productivity was found in prairie soil stored for 3 years in Alberta. Mycorrhizal infection was initially slightly quicker in comparable unstored soil, but infection in the stored soil caught up. In both cases it was rapid, and was attributed mainly to root fragments rather than spores, which were scarce in both cases. However, whereas *Glomus fasciculatum* was dominant in the undisturbed prairie soil, *Glomus mosseae* produced more spores in the stored soil, suggesting that it may have a greater capacity to survive stockpile conditions (Visser *et al*, 1984). But highly adverse effects were found in topsoil stockpiled for 5 years in Wyoming. Mycorrhizal establishment there, in a sandy clay soil low in organic matter was extremely low (Warner *et al*, 1987).

A different perspective was achieved in another surface mining site in Wyoming (Miller *et al*, 1985). Eight topsoil stockpiles ranging in duration of storage from 0.5 to 6 years were

sampled and bio-assayed for infectivity. There was no discernible decrease in infectivity during the first 2 years of topsoil storage, but the level then dropped by over 50%, recovered slightly and then remained at about the same level through to year 6. The topsoil storage piles had all been seeded with *Agropyron* spp., but at the time of sampling only those piles more than 3 years old had grass cover. Annual precipitation over the period of study was only 154 mm, and it is thought unlikely that the soil water could have recharged below the top 0.5 m. It therefore appears probable that some at least of the live propagules detected by bioassay in the lower soil samples (down to 2 m depth) may have been survivors from the time of the stockpiling, up to 6 years before, but this cannot be regarded as certain. The fungus here was of the *Glomus fasciculatum* type.

This evidence suggests that the infectivity of stockpiled soil can often be maintained for 2-3 years in dry conditions, though the balance of AMF species may change. It is consistent with the Australian inference in Section 3.5.3.1., that it is the wetting of disturbed bare soil, rather than the disturbance itself, that is mainly responsible for the loss of infectivity.

### **3.5.3.3. Dormancy and re-emergence**

Successful dormancy requires the ability to maintain life with minimal consumption of stored resources, to respond to a genuine opportunity to re-enter the active phase, but not to be tricked into premature activity by an apparent but not real opportunity. Arid and semi-arid environments commonly subject plants and their fungal partners to long periods, which may be seasonal or may be of unpredictable duration, during which growth is not possible. These periods are followed by windows of opportunity which are sudden and probably

quite short, triggered by rainfall, and sometimes but not always preceded by temperature or daylength signals.

AMF propagules have been found to remain viable for up to six and a half years in Illinois soil (Reeves *et al*, 1979, reporting an earlier finding by Gerdemann), but a decline in viability over period of a few years was shown in the Wyoming investigations cited above, and is widely documented.

The possible important role of the intact hyphal network under natural, undisturbed vegetation was mentioned above. The hyphal network of *Acaulospora laevis* maintained infectivity for 36 days in dry soil, after being detached from the plant roots, providing it was otherwise undisturbed, but disturbance of the soil severely reduced infectivity (Jasper *et al*, 1989). Plant roots can die back annually and then re-grow down the original root channels; fungal inoculum surviving in dead roots can then be an important source of infection of new roots (Friese & Allen, 1991). Hyphal fragments in broken pieces of dead root are an important inoculum type in disturbed as well as undisturbed soil; in long fallow disorder (cf. Section 3.5.3.1) it was not the cultivation but the occurrence of false breaks, rainfall in the absence of plants, which led to loss of infectivity (Pattinson & McGee, 1997). The possible role of intact extraradical hyphal networks surviving from the previous season is not clear (Jasper *et al*, 1989; McGee *et al*, 1997). Friese and Allen (1991) point out that hyphal types are specialized for their function; runner hyphae were observed to infect new roots, but absorptive hyphal networks were not. The reduction of infectivity following disturbance of soil (McGee *et al*, 1997) may be due to the disruption of infected dead root



systems rather than the destruction of extraradical hyphal networks, but there is some evidence from seasonally dry W Australian forest that diffuse fungal networks may maintain infectivity through extended periods of summer drought (Brundett & Abbott, 1994).

Different species of AMF appear to have different survival strategies (McGee, 1989). Fragments of dry root infected with *Glomus monosporus*, *Glomus fasciculatum* or *Gigaspora calospora* produced new hyphae and colonized seedlings, but similar fragments infected with *Acaulospora laevis* or *Glomus caledonium* did not (Tommerup & Abbott, 1981; Scheltema *et al*, 1987). *A. laevis* and *Entrospora frequens* have been thought to rely exclusively on spores as propagules (McGee, 1989), but Jasper *et al* (1993) report infectivity in hyphae of *A. laevis*, though they found that the infectivity declined rapidly after sporulation. Spores of some species of *Acaulosporaceae*, including *A. laevis*, have an obligatory dormancy period (6 months in the case of *A. laevis*), which would protect them against any false breaks occurring in their first dry season, but they appear to be fairly short-lived; spores of *Glomus* spp. have a much shorter dormancy (McGee *et al*, 1997; Scheltema *et al*, 1987.) Spores of *Gigaspora* (*Scutellospora*) *calospora* are only dormant for 6 weeks in dry soil, but being large they may have enough stored carbohydrate to survive a false break (Braunberger, Abbott & Robson, 1994). Staggered spore germination has been suggested as a possible survival mechanism (McGee, 1989).

### 3.6. Summary

Both AM and EM fungi show considerable intraspecific variation. In the case of AMFs this can lead to significant adaptation to local edaphic and climatic conditions and a number of studies have found local isolates, or in one case isolates adapted to less fertile sites, to be more effective in increasing plant biomass.

EMF typically associate with woody perennial hosts. Their mycorrhizas are substantial structures, apparently able to store mineral nutrients in the fungal sheath and maintain a supply to the plant during drought. They have an endurance strategy.

AMF are more opportunist; their flimsy structures develop quickly and they avoid drought stress by escaping into dormancy. Their spores, intact dormant hyphal networks and the infected fragments of dead roots all act as propagules, though not all AMF species necessarily regenerate from all three propagule types. There is conflicting evidence regarding the effect of cultivation on infectivity. In Australia, low-P cracking clay agricultural soils did not suffer a loss of infectivity unless there were false breaks (caused by rain during extended fallow), whereas disturbance of forest soils or other native perennial systems led to reduced infectivity even without false breaks, and it was inferred that intact hyphal networks may be the main AMF propagules in this type of ecosystem, whereas agriculture may tend to select for fungal species that propagate mainly by spores. In Somalia, shifting agriculture was considered to have been implicated in the greatly reduced infectivity of degraded land. In one survey in Spain, mycorrhizal activity was found to be low in currently cultivated land and only recovering very slowly in land which

had been abandoned by agriculturalists. However, another survey found high levels of mycorrhizal infectivity in former agricultural land, though the fungi were ineffective as symbionts for the native shrubby legumes the researchers were working with (cf. Section 3.5.3.1.). It is not clear how long had elapsed since agriculture ceased on the latter site. But the general conclusion is that cultivation or other disturbance reduces or changes the mycorrhizal fungal population, and in both cases there may be adverse effects on outplanted trees and shrubs.

It is thought that EMs have enzymes capable of sequestering P and N in organic combinations still in process of decomposition, whereas there is no evidence that AMs can do this. Instead, AMFs may depend more on interactions with other soil microorganisms such as rhizobia and phosphate-solubilizing bacteria. Both EMF and AMF have been found associated with pseudomonads, and these may have a role in the early stages of fungal development.

Where plants root very deeply to tap deep water-tables they may also be finding nutrients, and AMF and other microorganisms seem likely to be involved in complex interactions. In the light of this, absence or scarcity of rhizobia or AMF in the topsoil may be misleading. It seems possible that some AMF may specialize in deep soil functioning.

Desert studies in Wyoming, California and Namibia have found either most, almost all or all plants surveyed to be mycorrhizal, and coarse-rootedness (characteristic of legumes and C<sub>4</sub> grasses, key components of savanna) is positively correlated with mycorrhizal

dependency. These facts suggest that, if desertified land is myco-deficient, re-vegetation is unlikely to be possible without the concurrent re-introduction of suitable AMF.

### 3.7. Discussion

AMs are the key mycorrhizal factor in most dryland recovery situations, though EMs have a part to play, particularly in *miombo* or former *miombo* areas. Mycorrhizal fungi appear to be ubiquitous in semi-arid regions, except where disturbance has caused temporary or long-term disruption to normal rhizosphere interactions. This does not justify premature assumptions of mycorrhizal dependence, but does offer grounds for shifting the burden of proof. If cheap and simple mycorrhization procedures can be developed and promoted, there is a case for arguing that they should be applied unless there is evidence indicating otherwise, since the probability is that they will be beneficial or innocuous. In other words, it may be wise to regard the complex network of interdependent organisms present around the roots of plants in natural soils as a likely ally rather than a probable enemy, and to integrate nursery-produced plants into this network as early as possible. This is borne out by the improved survival and growth often reported for mycorrhizal plants, and in particular by their improved resistance to pathogens (cf. Section 3.1).

The selective advantage which EMFs appear to possess in certain stressful climates and on some nutrient-poor soils raises the question whether they might have a special role in the recovery of desertified land. Figure 5 suggests that their competitive advantage does not extend to the drier end of the semi-arid rainfall gradient, and certainly not to the areas classified as arid, but their predominance in the *miombo* dry woodland of Central Africa

and in Australian mallee, and their firm position in Portuguese-Spanish cork oak savanna suggests that they may well have an important part to play. The fact that eucalypts and *Uapaca* species commonly use AM mycorrhizas initially and are subsequently integrated into the EM system makes them particularly interesting and may be an important advantage. On the other hand, eucalyptus trees and miombo woodland are widely feared; the eucalypts for the effect they may have on the water-table, the miombo woodland as the home of the tsetse fly, so any plans involving these species need to address the perceived risks. However, the fruit-bearing *Uapaca kirkiana*, grown in orchards, is acceptable and indeed popular, and it would be interesting to attempt to reproduce its AM-EM sequence experimentally.

The fact that cultivation or deforestation can be expected to change the AMF species composition or drastically reduce propagule levels needs to be borne in mind when trees are to be outplanted on disturbed sites; infectivity may be low, or propagules present may not be appropriate or effective symbionts.

Very deep taproots are a key feature of some prominent and valuable arid and semi-arid plant species, and the limited evidence available suggests the possibility that certain AMF species may be adapted to accompany the taproot as it penetrates down to the region near the water table. *Glomus fasciculatum* and *Gigaspora margarita* may be such (cf. Section 5.4), and might repay investigation, as might the apparent synergistic effect of certain AMF species and phosphate-solubilizing bacteria.

Legumes and C4 grasses both tend to be coarse-rooted and to be relatively mycorrhizal-dependent. They are commonly found together in tropical savanna, and their mycorrhizal dependency appears to be positively correlated with increasing aridity and nutrient-poverty. Savanna legumes are typically AM, whereas the tropical Caesalpinoideae are non-nodulating and EM.

AMF species appear to differ in their survival strategies, and this too might repay investigation. Practical measures to foster AMF effectiveness are the maintenance of plant cover and the minimizing of soil disturbance, particularly prior to inadequate rain, where that can be predicted. Some AMF species appear to be better adapted to undisturbed soils, whereas others respond positively to cultivation; *Glomus fasciculatum* was dominant in undisturbed prairie, but might be displaced by *Glomus mosseae* under cultivation. These differences tend to argue in favour of mixed rather than single AMF species inoculation, particularly in agroforestry situations.

Where mycorrhizal inoculation is under consideration the initial presumption should be that local isolates or inoculum collected from less fertile but otherwise comparable sites are likely to be most appropriate. Forest soils or previously undisturbed natural grassland should be used as inoculum sources, not agricultural soils. Inoculum must be freshly gathered and then constantly cultured. The timing of procedures needs to be synchronized with the rainy or growing season.

EM inoculation needs to take account of the different early and late stage fungal partnerships that occur in nature. This poses a dilemma in the tree nursery. Early stage inoculation first followed by late stage inoculation at outplanting time might be the solution, but this would need verifying.

Beneficial interactions with other soil microorganisms may also be important. Synergy between AMF and *Rhizobium* or *Frankia* is widely documented, and in some circumstances other bacteria may participate symbiotically. This possibility needs to be taken into account, and argues in favour of using non-sterile local soil or sophisticated multiple inoculation.

#### **4. The search for solutions**

The obvious first solution for any problem is simply to remove the cause, and this may be enough. Exclosure or restricted use has frequently been applied as a remedy for prolonged overgrazing or wood harvesting, sometimes with striking success. Tanzanian experience in the Kondoa Eroded Area (Section 4.1.) is illuminating in several ways, and is supported by evidence from Kenya and NE Nigeria (Section 4.2.). In other areas, desertification appears to have progressed too far. An example of a failed exclosure experiment in the Sahel was quoted in Section 2.1. (Thomas, 1997), and the term 'irreversible' appears in the literature. In N Africa, Chile and SE Spain the degradational processes appear to be widespread and longstanding. The natural resilience of dryland ecosystems has gone. A threshold has been crossed. Workers in Tunisia offer a model of desertification conceived in terms of the crossing of degradational thresholds. The model both uses and qualifies the concept of irreversibility. These important ideas are discussed in Section 4.3.1., and key Spanish research focussing on microbial deficiency and remediation is reviewed in Section 4.3.3. The research being reviewed in these sections suggests that recovery is not impossible, but will be much harder to achieve and will require close attention to plant-microbe interactions in the soil. A low-cost method of fostering these, described in the final section of this chapter appears to offer an exciting way forward.



#### 4.1. Kondoia and the HADO Project

The area designated Kondoia Eroded Area (KEA) is situated in the Irangi Highlands to the north of Dodoma. Dodoma Region is the heart of Tanzania's drylands (Figure 6). Average annual rainfall is 600-700 mm. The rainy season is October-May. Rain falls in torrential storms; up to 77 mm can fall in a few hours. The area has a rolling topography between 1300 and 2000 m.a.s.l. Infiltration is poor, and up to 60% of precipitation can become runoff.

Extensive deforestation programmes for tsetse control were carried out in Kondoia (and elsewhere in Tanzania) from 1927, and by 1952 it was claimed that tsetse flies had been almost eliminated from Kondoia. The region experienced an explosion of human and bovine populations and this led to breakdown of the traditional bush fallow system, excessive grazing and wood-gathering pressure, and cultivation on sloping sites. Kondoia presented the most dramatic example of soil erosion - innumerable gullies, some up to 20 metres deep, and sand-choked rivers. The vegetation is mostly bushland, with isolated bushed grasslands and also some vestiges of the *Brachystegia-Julbernardia* (*miombo*) woodlands that survived the general deforestation measures.

The Government-sponsored HADO (Hifadhi Ardhi Dodoma) project initially focussed on soil conservation measures such as contour bunds, check dams, seedling production and tree planting, but this approach proved too slow and expensive, so in 1979 de-stocking was applied to 1200 km<sup>2</sup>. This led to a dramatic regeneration of the vegetation, less sediment in the streams, rivers narrower, more stable and flowing later into the dry season, and wells

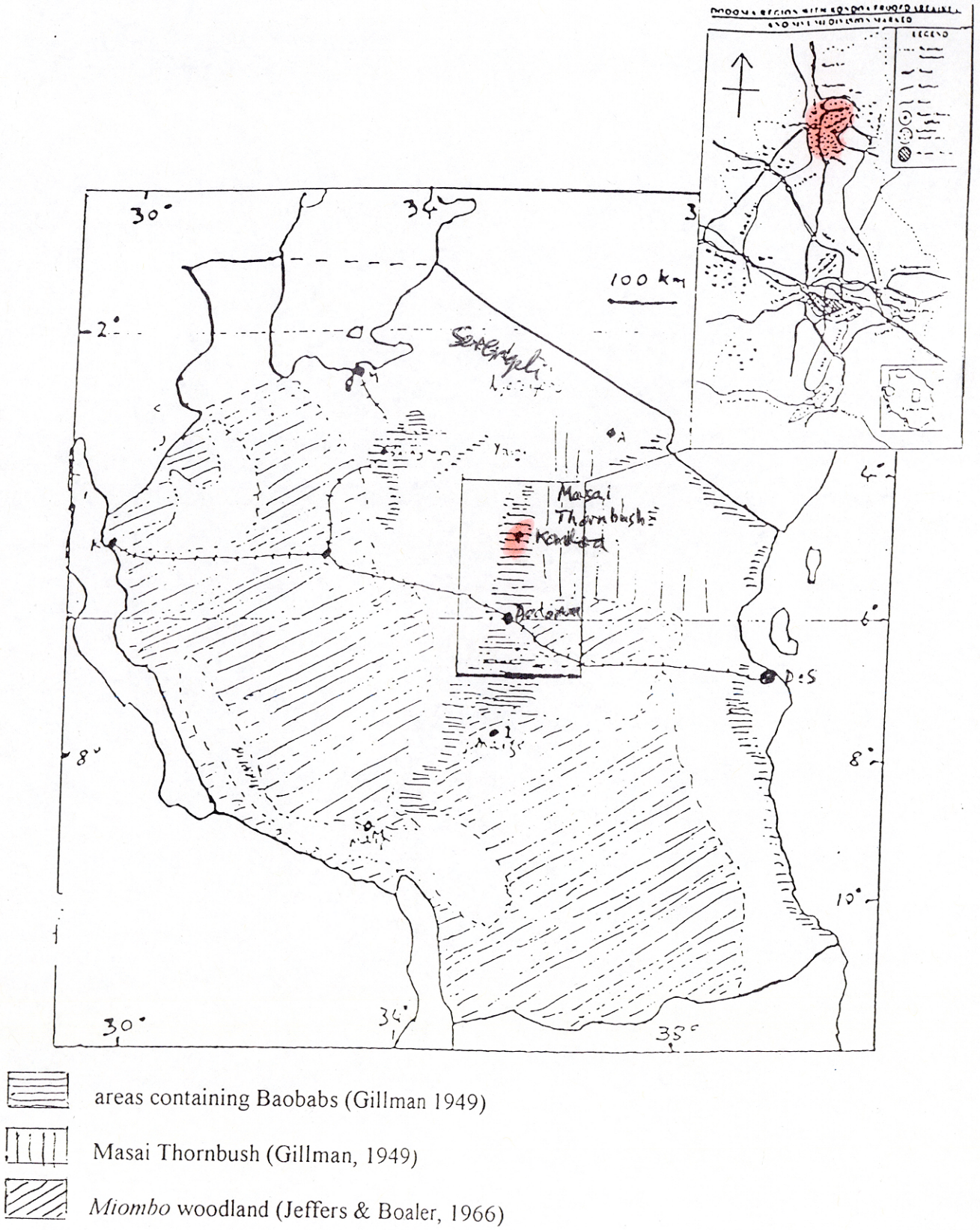


Figure 6. Kondoia Eroded Area of Tanzania.

that previously dried up in the dry season yielding water all year. Clearly, in this instance, in spite of serious damage arising from human misuse, the natural resilience of the ecosystem, including its mycorrhizal fungi and other symbiotic microorganisms, had not been greatly impaired.

But although de-stocking was an ecological success, it was not in its original form a social success. It was seen as colonialist, a solution imposed by Central Government. Removing the livestock merely transferred the problem somewhere else, and arson and illegal grazing were common. More sensitive and participative approaches, involving awareness-raising and a change of emphasis from pure conservation to broader-based husbandry - stall-feeding, extension services, beekeeping - replaced top-down interventions. (Mbegu, n.d.; Mungongo, 1991; Christiansson *et al*, 1991; Mgeni, 1992; Kikula, 1999).

#### **4.2. 'More people, less erosion'**

A closely documented case study of Machakos District, SE Kenya, assembles convincing evidence that population increase is compatible with recovery from environmental degradation. As in Kondoa, the key factors appear to be the development of agroforestry and soil conservation skills, stall-feeding of livestock, and family ownership of small farms (Tiffen *et al*, 1994). A similar situation is reported from NE Nigeria, where relatively degraded Sahelo-Sudanian shrub-grasslands were converted to permanent farmland. Sustainable productivity was found to be higher after conversion. Small-holders were observed to conserve and replant useful trees, stall-feed animals in the rainy season, use all residues, and apply manure to fields. The general effect was of parkland (Mortimore *et al*,

1999), and the conclusions drawn were that sustainable and more productive land-use systems had been developed.

It seems likely that even though these areas have a recent history of varying degrees of degradation, they retained enough plant resources and soil microorganisms to support productive agroforestry. Introduction or deliberate manipulation of mycorrhizal fungi may confer added advantage but is presumably not necessary, except possibly if non-local tree species are to be introduced. It should be stressed that the situations described here are mosaic-type situations; the degraded Kondoan woodland still had a range of trees, Machakos was an *Acacia tortilis*-grass scrubland before conversion; the Nigerian sites had scattered survivors of the natural woodland (*Adansonia digitata* and *Faidherbia albida*) as well as regenerating shrubs. Conversion of such areas into smallholdings with trees protected and planted for their useful products and for their value as boundaries and windbreaks could be expected to promote rather than undermine the activity of mycorrhizal and other potentially symbiotic microorganisms.

#### **4.3. "Thresholds of irreversibility"**

A more recalcitrant situation is reported in other areas, and the concept of thresholds of irreversibility has been developed to describe it (Aronson *et al*, 1993a/b).

#### 4.3.1. North Africa

A series of studies have been conducted on a sandy plain with 100-200 mm average annual rainfall at Menzel Habib in southern Tunisia. Thought to have been an arboreal steppe several millennia ago, with a tree stratum including *Acacia tortilis* ssp. *raddiana*, thousands of years of firewood harvesting, cereal cultivation and chronic overgrazing converted the area into a shrub-steppe which, in its comparatively intact state, comprised a sub-shrub layer of *Rhanterium suaveolens* and *Artemisia campestris*, perennial, rhizomatous and bunch grasses, and a large number of annual grasses and forbs. From 1956, due to a change in the law of land ownership and increased population pressure, areas formerly considered uninhabitable have been settled, and there has been a rush to establish ownership of land by cultivating it even if it was unsuitable (Aronson *et al*, 1993a /b).

Aronson and associates developed a model of ecosystem degradation highlighting thresholds of irreversibility and possible ameliorative goals and pathways. Thresholds of irreversibility were degradational changes from which an ecosystem could not of itself recover within a human timescale. Targetted human intervention might bring about a re-crossing of these thresholds, but options and methods needed careful consideration. Intervention could aim at restoration, rehabilitation or re-allocation. The aim of restoration was to return the degraded ecosystem to a pre-existing undamaged state, reassembling the original species inventory, ecosystem structure and dynamics or at least directing it back towards an approximation to this state. The aim of rehabilitation or reclamation was to repair damaged or blocked ecosystem functions, for human benefit, as rapidly as possible, but the principal model was still a simplified version of the pre-disturbance ecosystem or a

comparable alternative 'steady state'. In contrast, re-allocation assigned a new use, assuming a permanent managerial role for people, and ongoing inputs.

The experimental objective adopted for Menzel Habib was rehabilitation. The following key objectives were defined:

- reconstitution of the soil seed bank
- re-stocking with organic matter and microorganisms,
- re-conditioning of soils,
- restoration of hydrological functioning.

The loss of species considered to be 'keystone species' was thought to be a degradational change across a threshold of irreversibility, and it was hypothesized that the reintroduction of a suite of presumed keystone species would accelerate rehabilitation by facilitating the reintroduction and establishment of additional native species, that is, it would 'jump-start' a recovery process which would then acquire its own momentum. So the first step was to be the reconstituting of a simplified steppe dominated by *Rhanterium suaveolens*, suitable for limited and controlled grazing, such as existed elsewhere in the region (the ecosystem of reference).

The experimental site was superficially ploughed and re-seeded with 4 species which appeared to be keystone species in the ecosystem of reference, *Rhanterium suaveolens*, *Stipa lagascae*, *Cenchrus ciliaris* and *Plantago albicans*. After 3 years, plant cover, total biomass and number of species present were greatly improved, and this was very



reasonably considered to demonstrate that one threshold of irreversibility had been re-crossed and a considerably higher level of productivity achieved. This level could support light grazing, and indeed depended on it.

However, further progress was considered to be blocked by another threshold of irreversibility. In the degradation process, the *Rhanterium suaveolens*-dominated shrub-steppe appeared to have arisen only with the loss of the nitrogen-fixing acacias and the perennial grasses that dominated and characterized the original 'arboreal steppe', and of their microbial partners. So a further programme was started. This included the reintroduction of *Acacia tortilis* ssp. *raddiana*, together with rhizobium and mycorrhizas (Le Floch *et al*, 1999). Details of this very interesting stage of the experiment are not yet available.

#### 4.3.2. Chile

The same model has been applied in studies of a large area of dryland in central Chile (Ovalle *et al*, 1995; Aronson *et al*, 1993a/b). The original vegetation was sclerophyllous matorral (maquis) but is now generally degraded and impoverished in fertility and species diversity. Over 2 million hectares are considered to be in crisis. The progressive decline in productivity (now barely a third of what might reasonably be expected) is attributed to severe and chronic over-grazing and inappropriate cultivation practices leading to soil exhaustion, compaction, and poor infiltration. Cereals are followed by a fallow period ranging from 2-20 years. During fallowing, thorny scrub (espinal) dominated by *Acacia caven* returns, but the understorey consists mainly of exotic and some native annuals of

little forage value. Almost everywhere, species diversity and the soil seedbank display a degree of impoverishment which suggests that a threshold of irreversibility has been passed, leaving an ecologically blocked system, with little or no secondary succession. Most espinal soils are reported to be badly eroded, with microbial activity practically nil in many places. The nitrogen-fixing capacity and useful out-of-phase phenology of *A. caven* are rarely put to good use.

Ovalle and associates point out that a substantial population depends on subsistence-level agriculture and animal husbandry for their livelihood, so ecological improvement has to be accompanied by economic benefit, short- as well as long-term. In studies conducted mainly in the moister, more southerly sector (annual precipitation 600-800 mm), they evaluated a range of possible treatments based on the introduction or reintroduction of nitrogen-fixing legumes, both annuals and perennials, together with appropriate rhizobacteria. They believe that selection of suitable *Rhizobium* and mycorrhizas is essential if the performance of nitrogen-fixing plants is to be optimized. Preliminary work has been done on selection of *Rhizobium*, but not, as yet, on mycorrhizas apparently.

*Medicago polymorpha*, a naturalized annual legume, is widespread and valued, and one promising strategy is based on sowing this or other annual legumes as a regular part of a ley farming system, rotating it with cereals (e.g. 3 years under *M. polymorpha* which is self-seeding after the first year, followed by one year of wheat). This strategy can be either a preliminary to rehabilitation (the reconstituting of a more productive and diverse thorny scrub yielding better forage and grazing) or a step towards a definitive reallocation of the



improved land to agroforestry. 59 provenances of *M. polymorpha* were tested, and the more northerly provenances flowered much earlier than the southerly ones, a key factor where the growing season is short. This suggests that, in Chile, northern provenances might prove advantageous in the south (Ovalle *et al*, 1995). However, this, if true, probably results from the unusual dimensions of Chile; researchers in Mediterranean and Near Eastern countries recommend local provenances of this and other species of *Medicago* as an effective first stage in the rehabilitation of degraded dryland (Bounejmate *et al*, 1992; Ewing, 1999).

Alternative strategies tested involved either the protection, replanting and tending of elite specimens of *Acacia caven* or the comparative testing of *Acacia saligna* and other nitrogen-fixing trees or shrubs, together with appropriate rhizobia. The *A. caven* strategy produced striking results on one site; a strong positive correlation was found between *A. caven* cover and the production and pasture value of herbaceous phytomass. A growing period 25-35 days longer under the acacias than in the open was observed. *Chamaecytisus proliferus* var. *palmensis* (Tagasaste) produced 10 times more phytomass than any of the other species tested. This alternative strategy was regarded as of long-term importance but risky and costly at present due to the degraded state of the land and the large numbers of (introduced) rabbits and hares (Ovalle *et al*, 1995).

It would be interesting to compare the mycorrhizal and rhizobial status of the *A. caven* on the site where its canopy appears to promote understorey vegetation of high pasture value with that of the acacias in the more general highly degraded fallows where the understory is

impoverished and ruderal. It seems possible that the region may harbour pockets of effective and potentially valuable microsymbionts which could have an important role in the rehabilitation of the badly degraded areas, areas which probably retain only very depleted populations of microsymbionts.

#### **4.3.3. Southeast Spain**

With one important exception, the situation in southeast Spain closely parallels that found in the degraded drylands of central Chile and North Africa, and a large body of Spanish research focusses on AMF presence, which appears to be ubiquitous but often only at levels too low to be effective. The difference is that in Spain there has for the last 50 years been a steady trend away from agriculture on marginal land, while in North Africa in particular the same period has seen ever-increasing pressure on fragile marginal land from a rapidly growing human population. So the solutions may be different, but the history and the problem appear common to all three areas, and it seems likely that research carried out in Spain may cast useful light on other areas where AMF may also be present but very depleted.

Jeffries and Barea (1994) stress that sustainability of soil-plant systems requires a balanced, functional below-ground microbial ecosystem. Mycorrhizal fungi are key participants. Their hyphal networks are ideally placed to scavenge and recycle nutrients from dying plants, thus closing nutrient cycles, and their biomass constitutes a pool of organic carbon. They also help to stabilize soil aggregates, which is crucial for soil conservation. Leguminous plants are also essential components of a sustainable system.  $N_2$  fixation is a

key source of nitrogen, but is dependent on the supply of phosphates and other nutrients; mycorrhizal associations improve the supply of nutrients both to the plant and for N<sub>2</sub> fixation, so nodulated legumes with mycorrhizas are specially adapted to cope with nutrient-poor situations.

A series of research projects centred on SE Spain has therefore focussed on the establishment or re-establishment of exotic or indigenous woody legumes. A four-year trial involving two indigenous and four exotic woody legumes, each with appropriate rhizobial and mycorrhizal inoculation, found that only the indigenous legumes were able to become established in a representative desertified site in the province of Granada. *Anthyllis cytisoides* was judged to be the most promising; the mycorrhizal inoculum used with it was an unidentified *Glomus* species isolated from the rhizosphere of almond and multiplied in a trap-pot with onion (the procedure is described in Section 4.3.4.). The rhizobial inoculum was G4. A reclamation strategy based on inoculated *Anthyllis cytisoides*, planted in random groups, was therefore proposed. This was seen as an artificial acceleration of natural regeneration processes (Herrera *et al*, 1993). The shrubs would act as “islands of fertility” (E.B. Allen, 1991) which would serve as sources of inoculum for the surrounding area and improve N nutrition for non-N<sub>2</sub>-fixing vegetation.

However, experiments using soil inoculum and seed from a similar site in Almería found that though indigenous AMF achieved high levels of colonization of *Anthyllis cytisoides*, the resulting mycorrhizas were relatively ineffective in promoting plant growth, whereas augmentation with the exotic *Glomus intraradices* did promote growth. It was pointed out

that the site was formerly agricultural land, and though it was now being colonized by plants such as *A. cytisoides*, the fungi present might be adapted to crop plants, and might not be functionally compatible with native wild plants (Requena *et al*, 1996). Soil disturbance tends to select for AMF species that depend mainly on spores or root fragments rather than undisturbed hyphal networks for their propagation (cf. Section 3.5.3.1.), and heavy use of agricultural fertilisers (admittedly unlikely in this particular case) might well select for fungi functioning almost as parasites rather than mutualists

Further trials by Requena and associates drew attention to an additional layer of complexity, already alluded to in Section 3.4. They tested *Glomus coronatum*, native in the field site, against the exotic *Glomus intraradices*, this time with a range of rhizobia and of plant-growth-promoting-rhizobacteria (PGPR) in double and triple combinations. The growth response of *Anthyllis cytisoides* to the different combinations varied widely, but some treatments appeared highly advantageous, and the native AMF proved more effective than the exotic one in co-inoculation treatments when combined with a particular native *Rhizobium*, but not otherwise. Addition of PGPR reduced plant growth in that case, but the triple combination AMF + *Rhizobium* + PGPR gave the best results in most other cases. So a revegetation strategy based on the management of mycorrhizas, *Rhizobium* and PGPRs was recommended, and it was stressed that local isolates must be involved (Requena *et al*, 1997).

Spanish, Portuguese, Greek and British researchers are currently collaborating on an EC-funded project for the Restoration of Degraded Ecosystems in Mediterranean Regions

(REDMED) (Green *et al*, 1999). The project addresses the restoration of degraded marginal lands at risk from erosion and desertification, using native sclerophyllous evergreen trees and shrubs. Work on nursery production of these plants will include the development of a detailed methodology for all stages of mycorrhizal inoculation; isolation of fungi, multiplication, characterization, selection, production of inocula and inoculation of seedlings. The nursery management of species that develop a long taproot at early nursery stage will also be studied; root-pruning or air-pruning (by the use of open-bottomed containers) has often been applied, to avoid root spiralling, but either procedure attacks the natural survival strategy of species adapted to seasonal drought, as has been pointed out by workers in Tanzania (Munyanziza, 1994; Munyanziza & Oldeman, 1996). Both long containers and direct seeding into the field sites will be evaluated. This work may well produce results of direct relevance to East Africa, where the domestication and propagation of long-taprooted indigenous fruit and timber trees is an important but demanding objective.

#### **4.3.4. A low-cost method of mycorrhizal inoculation**

Recent work in Kenya demonstrates that trap-pot techniques could be used to improve nursery and out-planting performance in typical tree nurseries, without recourse to sophisticated procedures or equipment. Where soil is used in the potting mix, some mycorrhizal infection of seedlings is likely, but, particularly in desertified areas, propagule concentrations are likely to be low (Michelsen, 1992; Michelsen & Rosendahl, 1989).

The method tested in Kenya (Munro *et al*, 1999) involved growing bait plants of maize (*Zea mays* L.) and cowpea (*Vigna unguiculata* (L.) Walp.) in soil harvested from under mature trees of *Acacia tortilis* or other suitable species. After 6 weeks, a mixture of washed and chopped roots from the bait plants and soil from their containers was used to inoculate 20 day old seedlings of *A. tortilis*. Topsoil which had supported herbaceous vegetation was also used in the potting mix. Inoculation promoted mycorrhizal formation, and after 24 weeks plants from all the inoculation treatments were significantly larger than the controls. The team point out that these techniques require no long-term maintenance, no sterilization and no specialized equipment or methods, and could easily be taught through extension programmes. It has been suggested that the mixture of indigenous AM fungi which is likely to be transmitted may be a long-term advantage for trees, enhancing their performance under a range of conditions, though persistent effects of inoculation on growth in the field have not yet been demonstrated, and it is thought that the advantages of inoculation are most likely to occur in the nursery and during the establishment phase (Mason & Wilson, 1994).

The method is currently being tested at a desertified site in Almería (Hicks and Villalain, pers.comm.). The indigenous leguminous shrub *Retama sphaerocarpa* is a tenacious and conspicuous component of the natural vegetation, and fosters a dense understorey of annual and perennial herbs under its canopy (Moro *et al*, 1997; Pugnaire *et al*, 1996). As the key element in 'fertile islands', it is expected to be a source of good mycorrhizal inoculum, and of *Rhizobium* and other symbiotic microorganisms. *Anthyllis cytisoides* and *Stipa tenacissima* rhizosphere soil is also being tested. The *S. tenacissima* soil revealed a richer

and more diverse spore population, an interesting finding given that *S. tenacissima* is seen as a keystone species.

#### 4.4. Discussion

Desertification is closely linked with soil erosion. The generation of soil in the C horizon (Richter & Markewitz, 1995) and the loss of soil particles from the surface by erosion are normally constant but extremely slow processes which need to be in balance. Where catastrophic rates of soil erosion arise and are allowed to continue unchecked until a substantial proportion of precious topsoil has been lost it is likely that the productive potential of the land will have been dramatically reduced, at least in a human timescale. Such desertification can be considered irreversible either by natural vegetation succession or human intervention.

However, North African studies in Menzel Habib, an area thought to have suffered thousands of years of damaging misuse present a more encouraging picture. Research teams there hypothesize that losses of keystone species have led to a degraded and less productive ecosystem. These losses constitute thresholds which could not be re-crossed by natural processes, because key plant and symbiont species were either totally absent or so depleted as to render them unable to recover to effective levels. But, for these workers, the problem suggested the remedy; if keystone species could be identified it might be possible to re-establish them, and this would constitute a re-crossing of the “threshold of irreversibility”. The keystone species could be either dominant in former less degraded vegetational stages or introductions capable of playing a key role in a rehabilitated or re-

allocated ecosystem. Such improvement might need to be brought about in stages (Aronson *et al*, 1993a/b; le Flo'h, *et al*, 1999). The reintroduction of particular annual legumes has been proposed as a first step by several workers; the reintroduction of dually inoculated *Acacia tortilis* ssp. *raddiana* was a second not a first stage in land rehabilitation at Menzel Habib.

This two-stage strategy seems to run counter to "islands of fertility" theory, and to the fallowing/rotational woodlot strategies which facilitate legume tree re-growth to enable soil to recover fertility for cropping. It raises the question whether compatible rhizobia are already present where medicks etc are to be sown. Also, AMF are thought to support rhizobia (by facilitating a P supply) not the other way round. It may be that AMF (and rhizobia?) are present and appropriate for annual legumes, but that symbionts suitable for leguminous trees have been lost. There appear to be many questions and no clear answers here, but the first stage of the strategy at least appears to work.

The question of the irreversibility of the degradation stage grass steppe to shrub steppe merits special attention in view of the observation that alpha grass (*Stipa tenacissima*) can regenerate vegetatively but not by seed in the absence of shade (Puigdefàbregas & Mendizábal, 1998; Hutchinson, 1996) (cf. Section 2.2). Hicks and Villalaín (pers. comm., 2001) reported a varied and apparently richer range of AMF under alpha grass than under the thriving legume *Retama sphaerocarpa*.



Munro *et al* (1999) have shown that effective mycorrhizal inoculation could easily be taught through extension programmes and practised in local tree nurseries. This seems an obvious first step, likely to yield positive results in dryland recovery or improvement programmes in most areas where dryland degradation is recent, and in some areas where it is a longstanding problem. Appendix 1 sets out a detailed protocol for the procedure. Situations where this simple solution did not work could then be identified and subjected to more sophisticated study.

The procedure advocated by Munro *et al* has the added advantage that, where the inoculum source is a legume, the trap-pot culture deriving from it may well contain suitable *Rhizobium* as well as AMF, though researchers warn that the matching of a given legume with an effective *Rhizobium* can be a complex matter. The procedure also allows for the transmission of other potentially important organisms, such as PGPR and phosphate-solubilizing bacteria. It could also transmit pests and pathogens, so it is important to harvest wild inoculum from under healthy flourishing plants and to observe good hygiene in the nursery; this includes keeping pots off the ground.

## **5. Plants and symbionts with a potential role in anti-desertification strategies**

It has been argued (cf. Section 1.2.) that savanna and agroforestry are the most appropriate and resilient land-use systems for semi-arid regions threatened or damaged by desertification. This raises the question of the selection of suitable trees and tree-production procedures. In most but not all of the degraded drylands under consideration, the local populations need to win a livelihood from their land, so any measures proposed must be seen to offer fairly quick returns as well as any longer-term benefit.

In many cases the first option to be considered should be the exploitation of any indigenous tree species already present, since these may have been key elements in the endangered ecosystem. They are also likely to be adapted to the area and to be growing in association with beneficial soil microorganisms. In considering such species as candidates, the important questions are whether they are economically useful and valued by local people, and whether they are reasonably fast growing.

This chapter profiles a number of multipurpose trees and shrubs and indigenous or known exotic fruit trees which are likely to be attractive and suitable choices for dryland protection and reclamation. Mycorrhizal information is given where available, but it is apparent that in many cases little or nothing definite or conclusive is known; furthermore, most findings quoted are from single trials in particular sets of circumstances, and more extensive testing would be necessary before general conclusions on mycorrhizal dependency could be drawn. The profiles are summarized in a table at the end of Section 5.3.

## 5.1. Acacias

This large genus has a pan-tropical distribution, and is particularly associated with hot dry regions. African acacias are thorny (unlike the Australian species), and are valued, particularly by pastoralists, as a source of nutritious pods, fuel and other wood products (Barnes, 2001). Barnes considers them as intermediate in plant succession, able to colonize degraded land and restore fertility to eroded and compacted soils and to pave the way for a succession which would, in the absence of heavy human pressure, eventually reinstate the climax communities. This constitutes a strong case for their use in anti-desertification measures. He points out that with present human population levels, the reinstatement of natural climax communities is not a realistic objective, but argues that acacias still have a valuable contribution to make to agricultural productivity in some of the most problematical parts of Africa (Barnes, 2001).

### 5.1.1. Acacias on the desert margins of Africa

*Acacia tortilis* is likely to be in the forefront of efforts to contain the encroaching desert. It is found in all countries fringing the Sahara, and is the tree that often extends furthest into the desert, producing large crops of nutritious pods under climatic and soil conditions that other useful species cannot withstand. It survives at very high temperatures and with mean annual rainfall as low as 40 mm. In these conditions it develops an extensive rooting system spreading to twice the width of the crown and to a depth of as much as 35 m. It favours young, alkaline and alluvial soils, and is found along seasonal watercourses in sandy soils, but will not grow on land subject to flooding, or on heavy clays (Barnes, 2001;

Kennenni, 1991). It is valued by pastoralists in dry areas of Kenya (with annual rainfall 400-800 mm) (Barrow, 1991); young saplings are very thorny and consequently are not browsed until well established, and the seeds are spread by goats and cattle (Schultka & Cornelius, 1997). The species was examined for AMF in the Kenya Rift Valley, and 12 types were found associated with its roots (Milimo *et al*, 1994). It was also selected by Munro *et al* (1999) for their trial of a low-cost mycorrhizal inoculation method, and responded equally positively to pot-cultured inoculum originating from the rhizospheres of mature trees of *A. tortilis*, *Prosopis juliflora*, or two *Terminalia* species (cf. Section 4.3.4). This responsiveness to a range of unselected mycorrhizal inocula promises well, though the authors also draw attention to the difficulty of nodulating this species. The other difficulty is that *A. tortilis* is seen by its users as a wild plant; raising and planting it are alien concepts.

*A. tortilis* includes several sub-species, each of which shows a high degree of local variation. A Botswana provenance of *A. tortilis* ssp. *heterocantha* is the most frost-tolerant, and *A. tortilis* ssp. *raddiana* is the least frost-tolerant. The latter is however dominant in the driest areas, extending from southern Morocco to southern Tunisia and into the Sahel. It is native in Senegal, where it has many quite dense populations in the north and west of the country, and is used by local people as fodder, charcoal and as shelter in agroforestry in areas with an average annual rainfall of 300-500 mm. It prefers a light, well-drained, sandy soil of at least moderate depth, and has been proposed for reintroduction as a means of restoring degraded dryland both to the north and south of the Sahara (Diouf & Grouzis, 1996; Le Floch *et al*, 1999). The Tunisian project specifically included mycorrhizal and

rhizobial treatment of the *A. tortilis* ssp. *raddiana* seedlings, but did not give details or results. It will be interesting to see, not only whether the reintroductions are biologically successful, but whether the approach wins public acceptance in an area where people have settled on and established individual ownership of desertified land which is unsuitable for cultivation and thought to have once been an arboreal steppe with *A. tortilis* ssp. *raddiana* as the dominant (Le Floc'h *et al*, 1999).

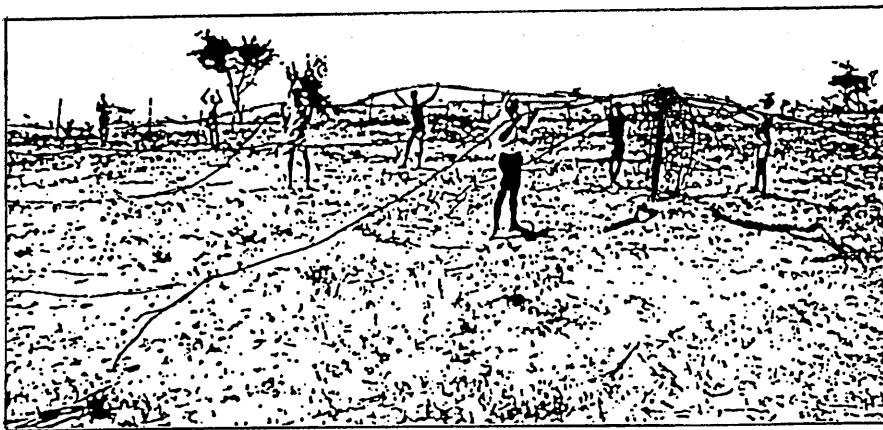
In a pot experiment with '*Acacia raddiana*' and *Acacia holosericea* using a sterilized low P soil of a type common in Senegal, *G. mosseae* + a *Rhizobium* increased shoot & nodule weights dramatically, but when the same soil was used unsterilized the increases were negligible (Cornet & Diem, 1982). This suggested that the indigenous AMF, present in the soil from seed-sowing time, were not beneficial to the growth of the plant, and also that the more effective *G. mosseae* which was subsequently applied as an inoculant was unable to replace the ineffective indigenous AMF which had already established themselves. The source of the soil is not given, but it may have been from an arable site with a modified AMF population.

Like *A. tortilis*, *Acacia nilotica* produces valuable pods under climatic and soil conditions seen as precluding other useful acacias. The timber is hard and durable, and is widely used for poles, beams, props, railway sleepers, agricultural implements, water wheels and boat building (Wickens, 1998). Unlike *A. tortilis*, it will grow on heavy clays or areas subject to seasonal flooding. It withstands high temperatures, but is frost-tender, particularly when young. Its sites are characteristically of high soil fertility, but it will grow on degraded or

saline sites and on industrial waste sites. There are a number of sub-species; one group prefers savanna, the other is more or less restricted to riverine and seasonally flooded habitats (Barnes, 2001). *A. nilotica* ssp. *tomentosa* grows abundantly in Eritrea in depressions subject to flooding, and is highly valued, protected and exploited by herdsmen. The inflorescences are a staple diet of young goats, and adult trees yield 80-100 kg of pods, which are stored, crushed and fed to livestock. The trees can remain in leaf all year unless drought lasts more than 10 months, and leaves too are used as forage (Audru *et al*, 1993). Studies of 10-year old acacia plantations in Senegal (annual rainfall 600-700 mm) identified *A. nilotica* as a suitable species for agroforestry (more so than *A. tortilis*), because of its high root concentration not only in the top 10 cm but also at depths 10-50 cm, indicating that it would take nutrients from below the crop rooting zone. A high level of mycorrhizal colonization was found at all depths tested and *Glomus mosseae* and *G. etunicatum* were identified (Ingleby *et al*, 1997). In an Ethiopian trial, *A. nilotica* was shown to benefit from an Italian dune isolate of *Glomus intraradices* (Michelsen & Sprent, 1994). Khan & Uniyal (1999) found that joint AMF and rhizobial inoculation of *A. nilotica* seedlings increased biomass by up to 40% after 6 months; a mixture of *Glomus mosseae* and *Glomus geosporum* was slightly more effective than one of *G. mosseae* and *Glomus aggregatum*. The *Rhizobium* used was not described, and the potting mixture may have been richer in nutrients than soil at a normal outplanting site. *A. nilotica* has also been successfully used in rotational woodlots in Shinyanga and Tabora, N.W.Tanzania, and information is being sought regarding the mycorrhizal status of the trees being planted there (Otsyina *et al*, 1996).

### 5.1.2. Other indigenous African acacias

*Acacia senegal* var. *senegal* replaces *A. tortilis* in slightly less dry areas, and is the dominant in a 300 km wide belt in the Sudano-Sahelian zone of sub-Saharan Africa, extending to Tanzania and across to the Middle East and India. It grows from sea level to 2000 m.a.s.l. in Kenya. It is common in hot, dry, barren regions, on rocky hills, hard pans, sandy flats and dunes with an annual rainfall of 200-350 mm., and widespread over the wider rainfall range 100-800 mm. on light soils and with even higher rainfall on heavy soils. Its root system is enormously extensive, both in depth and width, enabling it to take advantage of both light superficial showers and deep soil water (Figure 7).



**Figure 7.** Excavated root system of *Acacia senegal* growing in low sand dunes at Ed Dumokia, Kordofan Province, Sudan.

The taproot was excavated to 2.3 m, where it was 18 cm in diameter. The lateral roots, which were mainly between 20-30 cm below the surface, extended for a radius of 25 m and then turned abruptly downwards (photograph and measurements from Wickens, 1998, p.224).

Senegal, Niger and Sudan provenances of *Acacia senegal* produce gum arabic (Tanzanian provenances did not within the period of the trials). This tree is the preferred source of gum arabic, and is an important cash earner in areas where nothing else will grow; Sudan gets up to 15% of its foreign exchange earnings from export of this product. *A. senegal* was traditionally cleared for four years of cultivation and then left to regenerate as a 'gum garden' for 14 years, but this fallowing system has broken down due to population pressure. Wickens (1998) reports a number of large scale projects throughout the Sahel involving the planting of *A. senegal* as an anti-desertification measure as well as for increasing the production of gum arabic (Barnes, 2001; Fries, 1991; Milimo *et al*, 1994; Wickens, 1998). The seed is wind-dispersed (Anon., 1992).

*Faidherbia albida* (formerly *Acacia albida*) is found in a wide annual rainfall range (100-500 mm in the Sahel, 1000-1500 mm in the Sudano-Guinean belt, 400-800 mm in Kenya) (Dupuy & Dreyfus, 1992; Barrow, 1991). It has reverse phenology, leafing in the dry season, and this makes it complementary with farm crops as it makes its growth demands at a different time of year and the leaves and pods provide good dry season fodder (Ong & Leakey, 1999; Wickens, 1998). It occurs as scattered survivors of natural woodland in N.E.Nigeria in areas now used as permanent farmed parkland. Here and elsewhere it has been not only preserved but planted as boundaries and for its valuable products and beneficial effect on grain crops growing in association with it (Ichire, 1993; Boffa *et al*, 1996; Wickens, 1998; Mortimore *et al*, 1999; Barnes, 2001). Studies in *F. albida* parkland in Burkina Faso, with annual rainfall 550-600 mm, showed a striking positive correlation between tree cover and grain yield (millet and sorghum) on sites with canopy cover ranging



from 6% to 16%. The effect was more marked on infertile sites and in drier years (Oliver *et al*, 1996). Mycorrhizal aspects were not investigated in this study, but pot experiments with sorghum have indicated that inoculation with *Glomus intraradices* enhanced the growth of the sorghum under drought conditions (Ibrahim *et al*, 1990). In the light of that finding it seems reasonable to suppose that the *F. albida* trees among which the sorghum and millet were growing in the study by Oliver *et al* may have been harbouring permanent pockets of AMF which would be well placed to colonize successive sowings of crop plants

*F. albida* depends on deep water; the tap root can penetrate to a depth of 40 metres, but it also has a well-developed surface lateral root system. The rhizobial concentration has been found to be greater near the water table than near the surface in dry N.W. Senegal (Dupuy & Dreyfus, 1992). Roots of *F. albida* at both drier and less dry sites in Senegal were found to be more than 50% mycorrhizal, mainly with *Glomus* and *Gigaspora* species, though *Acaulospora* and *Sclerocystis* were also represented; some mycorrhizal roots were found around the water table, at depths down to 4.5m (Diop *et al*, 1994). In a more recent study at the same sites, Dalpé *et al* (2000) found four *Glomus* species (*aggregatum*, *caledonium*, *fasciculatum*, and *mosseae*) near the surface and *Glomus fasciculatum* and *Gigaspora margarita* at a depth of 34 metres at the drier (Sahelian) site. They recommended selection and propagation of high performance strains of indigenous AMF as an inoculum for *F. albida* seedlings intended for land rehabilitation. In an experiment in Burkina Faso, *Glomus aggregatum* and *Glomus manihotis* enhanced the growth of *F. albida* in the presence of added rock phosphate (Bâ and Guissou, 1996).

The West African/Ethiopian cluster is genetically distinct from the isolated populations of East and southern Africa, where its natural range has been exclusively riverine, regenerating on newly-formed sands and silt banks after flooding in areas which are sufficiently frost-free to enable plants to put on enough height to get above freezing temperatures. But it has also been found to grow very well away from rivers where the climate and soil are suitable. It needs freedom from competition by grasses during the establishment phase (Barnes, 2001), and failure of fast-growing types in Niger has been attributed to excessive stress put on the plants by the simultaneous demands of deep rooting and fast shoot growth (Ong, 1992). Seedlings, which produce a single taproot, survive drought in early years better than plants grown from cuttings, which make quicker initial growth but produce several taproots (Ouedraogo, 1993).

### 5.1.3. Australian acacias grown as exotics

*Acacia holosericea* needs a minimum of 500 mm annual rainfall in coastal areas or 600 mm inland. It is sensitive to long droughts but adapts well to most soils, even saline or water-logged ones. It makes fast initial growth, reaching maturation in two years. It tends to form dense clumps in disturbed places or near watercourses, but has poor coppicing ability (Cossalter, 1986; Fox, 1986). Inoculation with *Glomus mosseae* increased nodulation and shoot weight dramatically, (Reddell & Warren, 1986; Cornet & Diem, 1982). In a monospecific 13 year old plantation in the N. Soudanian belt of Burkina Faso (annual rainfall 800 mm), *Glomus aggregatum* was found to be the most common AMF, though *Acaulospora delicata*, *Glomus geospermum* and *Scutellospora gregaria* were also

present, and researchers suggested that local variant strains of AMF might be useful for the optimizing of N-fixation and plant growth (Bâ *et al*, 1996).

*Acacia mangium* will grow on difficult sites and has been used for rehabilitation of degraded sites outside Australia (Kessy, 1986). It grew very quickly and became the tree of choice for firewood in Burundi, though its coppicing response was poor (Salvator, 1997). It is normally AM but one provenance formed EM and grew well (Duponnois and Bâ, 1999). The presence of AMF was investigated in a monospecific 13-year old plantation in the S Soudanian belt of Burkina Faso (annual rainfall 940 mm, sandy soil), and six *Glomus* species were found, of which *Glomus aggregatum* was the most common; followed by *Glomus manihotis*, two *Scutellospora* species, *Acaulospora delicata* and a *Gigaspora* species were also found (Bâ *et al*, 1996).

*Acacia saligna* was probably the first introduction and has been considered to be the most successful Australian acacia in North Africa. Widely planted in Algeria from about 1870, and in Libya for dune stabilization from 1916, this species needs and is adapted to sandy soils, growing well on deep sandy soils with annual rainfall over 250 mm, and surviving with 200 mm., though its natural range in Australia is 600-1000 mm. Its salinity and cold tolerances are slight, and it is not found above 800 m.a.s.l., or where the mean daily minimum temperature of the coldest month is below 4° C. *A. saligna* is useful for forage or firewood; the long phyllodinous type gives better forage and the wide phyllodinous type gives better firewood. It does not appear to regenerate naturally from seed in Mediterranean areas. This is both a positive and a negative feature; it is not invasive, as

some exotic acacias can be, but this limits its usefulness in some situations (El Lakany, 1986; Zaafouri *et al*, 1995; Le Houérou, 2000). It performed poorly in trials at Dodoma and Malya (Tanzania), possibly due to altitude, soil type or absence of symbionts (Kessy, 1986).

*Acacia salicina* is very drought tolerant, growing well in annual rainfall 150-300 mm on poor gypsophilous soils in Tunisia, Libya and Israel. It is tolerant of slightly saline soils, and has a strong suckering nature which makes it an aggressive colonizer. *A. salicina* provides good fuelwood, but has limited use as fodder due to the high tannin content of the leaves (Fox, 1986; El Lakany, 1986; Le Houérou, 2000). It was reported to have performed satisfactorily in Senegal as fodder/fuelwood/windbreak (Cossalter, 1986).

#### **5.1.4. Acacias and the recovery of degraded dryland**

Acacias are well-known and valued as fodder and fuel sources in dry regions of Africa, and the opportunity to develop their use is most likely to occur where people are attempting to increase the productivity of degraded land by abandoning a fallowing system which has become too shortened to allow recovery in favour of permanent agroforestry, using parkland intercropping, protective boundary planting or rotational woodlots. Taking the NE Nigeria situation described in Section 4.2 as an example, the presence of scattered survivors of *Faidherbia albida* (a species profiled above, and with many positive features to recommend it) would seem to make this species an obvious choice in that region. Acacias respond readily to a wide range of AMF, and where members of the genus or other AM tree species are already growing naturally in the locality the simplest mycorrhizal

strategy is likely to be merely to promote awareness of the advantages of using freshly harvested soil from the rhizosphere of flourishing AM trees in the tree nursery (Jaenicke, 1999). Alternatively, a plug of rhizosphere soil could be put below the seed if it is being direct-sown. However, in view of the findings of Munro *et al* (1999), as well as the practical difficulty of obtaining enough rhizosphere soil without damaging the source trees, it would be very advantageous to promote the trap-pot method of inoculum multiplication described by Munro and his associates (and see also Appendix 1).

It would be useful to develop a protocol for inoculum and seedling production in these circumstances. Where the target species has reverse phenology, this may mean that mycorrhizal infectivity is high in the dry season, and that rhizosphere soil gathered then would be a good starter for trap-pot culturing. If the trap-pot stage could be completed towards the end of the dry season, seed could be germinated in fresh inoculum just before the onset of the rains, and the fast-growing seedlings would be ready for outplanting early in the rainy season. This is speculative; the feasibility of the timings would need testing, and the practicability of growing and irrigating trap-pot plants in the dry season needs considering.

## **5.2. Other savanna trees**

There are a number of other tree species that are either prominent and traditionally valued components of savanna vegetation in particular areas, and are likely to be havens of AMF and other symbionts, or species which have attracted widespread interest on account of their special qualities and characteristics.

*Adansonia digitata* (the Baobab) is widely distributed in the savannas and grasslands of tropical Africa, within an annual rainfall range of 100-1500 mm. It prefers sandy topsoils overlying loam, can tolerate poorly drained heavily textured soil, but not deep sands (Wickens, 1998). Belsky *et al* (1989) describe isolated mature baobabs and *Acacia tortilis* as features of the semi-arid savanna in Tsavo National Park in Kenya, the baobab being drought-deciduous and appearing to rely on very wide-spreading shallow roots, whereas the acacia had both a well-developed shallow root system and a very long taproot which gave it access to deep soil water. Both species appeared to function as islands of fertility. Working in Senegal, Bâ *et al* (2000) reported baobabs to be well colonized with AMF, both *Glomus aggregatum* and *Glomus intraradices*, but found them only marginally mycorrhizal dependent. The baobab is valued for its fruit and fodder production and also has medicinal uses (Buwalda *et al*, 1997; Maghembe, 1994), but it is very slow growing (Anon., 1993); it is important to maintain populations, but planting for the benefit of future generations would need to be done as a community or national responsibility. Mature specimens do not appear to be very mycorrhizal-dependent, but inoculation may well have a significant role to play in the establishment and early growth of replacement trees.

*Argania spinosa* is the dominant tree in SW Morocco, requiring an annual rainfall of 100-300 mm. and tolerating most soil types except drifting sands and waterlogged soils. The seeds germinate readily, and the young trees fruit within 5-6 years. The nuts contain an edible oil, and the fruits and leaves are eaten by livestock, particularly goats (Wickens, 1998).

*Azadirachta indica* (Neem) is native to India. It grows naturally on the edge of the Thar desert, with an annual rainfall of 300 mm, cold winters and very high summer temperatures, where it has been observed growing in a curious apparent symbiotic relationship with *Prosopis cineraria*, the *P. cineraria* having been planted and the younger neems having established naturally within 15 cm of the partner species. This phenomenon was found at about 30 sites throughout the research area (Arya *et al*, 1992). Neem has been widely adopted in agroforestry in dry areas of South India (average rainfall 450-600 mm), planted at about 86 trees/ha and intercropped with cotton, millet, sorghum, coriander or sunflower. The trees have an adverse effect on crops if the monsoon is late or below normal, and cotton can only be grown around trees under three years old, but the fodder and the nuts (which produce oil and fungicidal substances), and the timber more than outweigh this disadvantage. Trees start to bear seed at about 10 years of age. Farmers in Tamil Nadu keep trees of different ages on their plots to maintain a fairly regular flow of products and income, and usually cut the trees down after 10-15 years, but a few are left for much longer. The seeds of older trees are smaller but thought to germinate better (Vivekanandan, 1998). Kumar *et al* (2000) found the species highly mycorrhizal-dependent, supporting Habte *et al* (1993), who found *A. indica* highly mycorrhizal-dependent with *Glomus aggregatum*. Combined inoculation with *Glomus fasciculatum* and phosphorus-solubilizing bacteria was more beneficial to growth and nutrient uptake than single inoculation (Kalavathi *et al*, 2000). Neem is now also widely grown in sub-Saharan Africa; being deep-rooted, drought resistant and fast growing, it thrives on poor soils in semi-arid environments and has become popular in shelterbelt planting and in forestry. It forms 90% of the trees in 500,000

ha of forestry plantations in Nigerian savanna and 17% of total tree cover in the republic of Chad. Unfortunately it is seriously endangered by several pests in this region (Lale, 1998). Otsyina *et al* (1996) report promising results and a big demand for seedlings of this species after rotational woodlot trials in desertified areas of Shinyanga, Tanzania, where the young trees are intercropped with maize for up to three years.

*Calliandra calothyrsus* is a small leguminous tree originating in Mexico and Central America now used in many parts of the world as a protein-rich fodder, as fuelwood and in land reclamation (Lodoen, 1998). Research into effective rhizobial inoculants has been reported by Muok *et al*, (1998) and Lesueur *et al* (1996). Reena and Bagyaraj (1990) found *C. calothyrsus* highly responsive in biomass and P uptake to inoculation with a wide range of cultured AMF.

*Cordeauxia edulis* (All the following information is from Wickens, 1998). This is a nodulating evergreen shrub of the subfamily Caesalpinioideae, growing up to 3m high. to 3 m high. Locally abundant in SE Somalia and the Ogaden of Ethiopia in areas with 85-200 mm annual rainfall, it grows on compacted sand and loamy sand, is intolerant of water-logging but tolerant of slight salinity. It can survive two years without rain. The 'nuts' are a delicious staple food in the area; Somalians recognize two varieties, of which moqley bears sweeter and larger fruits. Wickens considers that they have potential as a dessert nut if plantations could be established. The fruits mature in 10-14 days after rain, but if the rains fail the fertilised ovaries remain dormant until the next rain. The seeds germinate rapidly and develop a deep taproot which must not be broken. Top growth is



slow, but shrubs can fruit after 3-4 years. It can be propagated from stem cuttings.

*Melia volkensii* occurs naturally in arid and semi-arid regions of southern Somalia, Kenya (Machacos area) and Tanzania. It is fast-growing and deep-rooted (so not unduly competitive with crops for soil moisture), and produces high quality timber as well as fruit, fodder and firewood. It is difficult to germinate, but farmers transplant seedlings that germinate in the corral after excretion by goats; root suckers are also used, and the Kenya Forestry Research Institute (KEFRI) has developed germination techniques (Blomley, 1994; Kidundo, 1997). Milimo *et al* (1994) report that it needs at least 450 mm average rainfall, and that there is marked variation in the performance of different provenances, but it roots from stem cuttings, so selection is possible. These sources do not give any mycorrhizal information.

*Moringa oleifera* is native to N. India, but is now grown widely in the tropics. Good growth has been achieved in Kenya within the average annual rainfall range of 400-1200 mm, in plantations from sea level to about 1200 m.a.s.l. It is arbuscular mycorrhizal, and the question whether it is mycorrhizal-dependent is a subject of research there (Odee, pers.comm., 2001). It has been reported to fruit up to 1500 m.a.s.l. (Jahn, 1991), and to grow up to 1800 m.a.s.l. (Odee). It germinates easily or can be propagated by cuttings, (branches 1-1.5 m long root readily and are used for hedging). However, trees propagated by cuttings are reported to have much shorter roots (Price, 1997). Seeds can be sown direct or transplanted after 2/3 months, the best time for planting being at the onset of rains (Sutherland, 2001; Odee). It is a slender, very fast growing tree (up to 4 m in its first year),

and fruits within a year. Being deep-rooted and with not too many shallow lateral roots, it appears suitable for intercropping. A short-stemmed variety, *M. oleifera* PKMI, has been developed in India and is often grown as an annual. The seed of *M. oleifera* are rich in high quality oil; 73% of this is oleic acid, which means that the oil approaches the quality and market value of olive oil.

A hundred years ago, Sudan Arab women discovered that moringa seeds were more efficient for the clarification of turbid Nile water than any other known plant material, and research has now shown that the presscake left over after oil extraction acts as a highly effective coagulant and antimicrobial agent, which tested well against the chemical reagent normally used in a river-water treatment works in Malawi (Folkard and Sutherland, 1996). The presscake is also a useful fertiliser or livestock food, while the leaves are a very nutritious, protein-rich human or animal food which can be harvested in the dry season, and the green pods are prized and marketed under refrigeration or canned among Indian communities (Folkard & Sutherland, 1996; Sutherland, 2001; Olson, 2001).

*Moringa stenopetala* is bushier in habit and slower growing than *M. oleifera*, flowering after two and a half years in the Sudan. It tolerates drier conditions and higher altitudes than *M. oleifera* and occurs naturally in the *Acacia tortilis-Delonix elata-Commiphora* spp. vegetation complex, which is often found on well-drained soils between 900 and 1200 m.a.s.l. *M. stenopetala* is thought to be native in semi-arid to sub-humid Ethiopia, Somalia and Kenya and to have originated in the lowlands but then to have been domesticated and used by paleonigrific peoples of SW Ethiopia in terraced gardens and fields up to 2000

m.a.s.l. It is drought-resistant, and has a natural range including areas with mean annual rainfall between 250 and 1400 mm, either bimodal or unimodal, but in the drier regions of Ethiopia it is planted in microcatchments to increase water supply and is also grown on irrigated terraces. Yields are mediocre on eroded, water-stressed soils, but good on well-watered, manured soils. *M. stenopetala* does not grow in swampy or waterlogged conditions. It tolerates high temperatures, and performs best in temperatures in the range 15-33° C, but does not tolerate frost (specimens being grown in Cairo lost their leaves and some branches died when winter temperatures dropped to 6-8° C, though the trees flowered the following year). Propagation in the Konso and Gidole highlands of Ethiopia is usually by seed sown towards the end of the rainy season, but seedlings growing naturally under mother trees are transplanted at the start of the rains, care being taken to dig out the taproot. Young trees up to 1.5 m tall are also moved to better sites (they are pruned back and the taproot reduced to 750 mm).

The leaves are the main product; they are a protein-rich vegetable available in the dry season. Tender pods are also eaten. The seeds are bigger than those of *M. oleifera* and have the same flocculating and antimicrobial properties (Jahn, 1991; Mayer & Stelz, 1993; Price, 1997).

*Parkia biglobosa*, *P. clappertonia*, *P. filicoidea* (all called **Locust bean tree**) grow naturally in Burkina Faso, northern Nigeria and southern Mali, in areas with a rainfall of 370-890 mm (Ichire, 1993), that is, the full semi-arid range as defined for summer rainfall areas like the Sahel. Tomlinson *et al* (1995) give the natural range of *P. biglobosa* as 5-15° N and 16-32° E and report that the trees are valued and protected in parkland farming

systems, but rarely actively maintained. Though this genus belongs to the Mimosoideae they found no evidence of nodulation in *P. biglobosa*, even where the intercropping groundnuts had active nodules. But roots were 85% mycorrhizal, and it was thought that this might enhance N-uptake and compensate for the lack of nodulation. Bâ *et al* (2000) found *P. biglobosa* to be moderately mycorrhiza-dependent, more so with an isolate of *Glomus aggregatum* from Burkina Faso than with a *Glomus intraradices* inoculum from Canada. There is conflicting evidence about the effect of these species on intercrops, but Ichire (1993) states that the taproots access deep water and nutrients and that the branch roots are also found more than a metre deep, which should minimize competition with crop plants. The pods and seeds, which ripen in the dry season are high in protein and nutritious for humans and livestock, and the researchers conclude that the presence of these trees on farmed parkland brings a clear overall benefit in productivity (Ichire, 1993; Tomlinson *et al*, 1995). Bagnoud *et al* (1995) agree, and consider that it is more profitable than *Vitellaria paradoxa* (Shea), with which it commonly associates. Reporting trials in Malawi, Maghembe (1994) recommends *P. filicoidea* for social forestry as being fast growing and having good survival in drought.

*Prosopis juliflora* is a nitrogen-fixing native of dry, tropical America, and has been widely introduced as a fuel and fodder tree. It is adapted to harsh conditions and has spread as a weed onto farm and pasture land, but in the right conditions and with proper management it has great potential in the reclamation of desertified land. It is currently being studied and developed in India (Pasiecznik, 2001). Working in Jodhpur (mean annual rainfall 360 mm, pH 8.1), Tarafdar and Praveen-Kumar (1996) found that indigenous AMF appeared to be

present at levels too low to be effective, whereas inoculation with *Glomus fasciculatum* improved colonization and plant growth. Comparative studies in 10-year-old plantation plots in Senegal found *P. juliflora* to have a lower root concentration and higher levels of mycorrhizal colonization than *Acacia tortilis* or *Acacia nilotica*, attributes which suggest its suitability for agroforestry, but it was also observed to have a more closed canopy with limited understorey vegetation, so the conclusion was that *P. juliflora* may be more appropriate for low fertility, degraded soils where soil amelioration is more important than intercropping (Ingleby *et al.*, 1997).

*Vitellaria paradoxa* (the shea tree) is a common traditional parkland/agroforestry tree in West Africa, and is often found associated with *Parkia biglobosa*. Its natural range extends from E Senegal through Mali and Burkina Faso to NW Uganda in regions with a mean annual rainfall of 500-1200 mm. Shea parklands rotate millet, sorghum, maize and cotton with fallow, but pressure on land has led to excessive shortening of the fallow periods. Study of intercrop yields showed that the trees reduced crop yield directly under the crown but increased it at the edge of the crown, so overall there was no negative effect on the sorghum, and the nuts and other tree products were a bonus. Overall productivity was found to be highest on the most densely tree-covered plots.

Shea are wild and variable. 26% were found to be consistently high producers, and 30% were worthless as producers. Farmers differentiate and select when clearing fallows, but they rarely plant specimens of superior value. Vegetative propagation is difficult; grafting and *in vitro* culture are promising. Trees mature slowly, taking 15-20 years to fruit.

The oil (shea butter) is valued and marketed for cooking and for its healing properties (shea nuts were the third largest export earner for Burkina Faso in 1985), but prices are low, collection and oil extraction are laborious, and shea populations are threatened by the African mistletoe, a plant parasite of the genus *Tapinanthus*, so the species is losing ground in W. Africa to other more easily produced vegetable oils. It does however have under-exploited potential in pharmaceutical applications, and remains a valuable resource (Bagnoud *et al*, 1995; Boffa *et al*, 1996; Lamien *et al*, 1996).

*Ziziphus mauritiana* (*jujube*) is widely grown in the Sahel, E Africa and India for fruit, nectar and pollen for honey bees, fodder, fuel and as thorny hedging. It is not frost tolerant, and is adapted to low or medium altitudes. It behaves as an evergreen where the temperature range is 20-35°C; fruit-set is best in these conditions, and is adversely affected by temperatures in excess of 35°C together with low humidity. It tolerates waterlogging for 1-2 months and thrives on any soil, including saline ones. If rainfall is over 750 mm or irrigation is applied, canopy development is vigorous and trees should be spaced at 7 or 8 metres; if it is under 500 mm, spacing at 6 metres is recommended. Water-harvesting and regular pruning is recommended. Expected yields are 30-50 kg of fruit per 5 year old tree if rainfall is 300-600 mm; this rises to 100-150 kg with irrigation. In severe drought (100-125 mm) the tree should still produce 10-15 kg. The species is fast-growing and can fruit after 18 months; fruiting at three years is normal. Selection for early fruiting and for fruit quality is important, and budding is recommended as the best method for multiplying improved cultivars. Local wild rootstock of e.g. *Ziziphus spina-christi* are recommended.

*Z. spina-christi* is suitable, grows widely in drier areas of N.Africa and the Middle East, and is itself a useful plant for windbreaks, dune stabilization, hedges, fuel and other wood uses, and for its edible fruits (Wickens, 1998). Seed for rootstock production can be sown into pits and the budding done the following year, or there is an accelerated technique sowing rootstock into polythene tubes and budding after 90 days (Vashishtha, 1997; Maghembe, 1994; Buwalda *et al*, 1997).

Bâ *et al* (2000) found *Z. mauritiana* highly mycorrhizal-dependent with *Glomus aggregatum*, but Kumar *et al* (2000) found the contrary with a mixture of *Glomus mosseae*, *Glomus fasciculatum* and *Glomus epigaeum*. Mathur and Vyas (1995) report that *Glomus fasciculatum* is among the commonest AMF in arid and semi-arid regions, and that it appeared to improve the resistance of the plant to pathogens by stimulating the production of defensive enzymes. The same workers found that *Glomus constrictum* improved the growth, nutrient uptake and transplanting survival of *in vitro* raised plantlets of *Ziziphus mauritiana* (Mathur & Vyas, 1999). The trials in Zambia, in which the young trees fruited at 18 months used forest soil in the potting mix to ensure the presence of microsymbionts (Maghembe, 1994).

### **5.3. Trees of the *miombo* dry forest**

*Miombo* areas (Chapter 1.1.2.2.) differ from savanna areas in two very important ways: (a) they are a mosaic of smaller AM plants and mainly EM dominants, whereas apart from ruderals, savanna plants are AM; (b) forest clearance of *miombo* woodland has been driven not only by the needs of shifting cultivators or pressure from growing populations, but also

by the fact that *miombo* vegetation has provided a favourable habitat for the tsetse fly. This problem was so severe that complete bush clearance was adopted as official policy in the worst affected areas. Shinyanga in NW Tanzania was one of these, and between 1930 and 1970 20,000 km<sup>2</sup> were cleared of all existing vegetation and re-settled. Cattle populations grew rapidly and cotton and other crops were encouraged. The result was disastrous; sheet erosion, soil degradation and shortages of fodder, fuel and construction wood. An area once covered in dense forest and long grass was reduced to semi-desert (Otsyina, 1993). To counter these problems, tree planting was promoted by extension services, but the fear of recreating tsetse habitat reinforces local preference for exotics rather than species which previously grew wild in the area. The local wild species are also perceived as slow-growing compared with exotic alternatives. However, *miombo* woodland is a rich source of a wide range of useful products - not only wood, fruits and honey but also edible fungi which grow under EM trees, and there is a strong case for the domestication and careful management of selected *miombo* species. The tsetse question is discussed by Frost (1996) and Chidumayo *et al* (1996) in the context of the ecology and management of *miombo* woodlands.

*Miombo* woodland is dominated by trees of the EM genera *Brachystegia* and *Julbernardia*, and these are prime sources of edible fungi, honey and wood suitable for charcoal. *Brachystegia spiciformis* is often the main component of the canopy. It prefers deep soil and is intolerant of waterlogging, so is often found on ridges and escarpments (Celandier, 1983). Campbell *et al* (1996) report a contraction of 350 km in the geographic range of the genus in under a thousand years, so consider it sensitive to fairly minor fluctuations in



temperature and moisture. Munyanziza (1994) studied natural germination of seed under two isolated mature trees of *B. spiciformis* growing in a field which was cropped with maize and beans, at a distance of two kilometres from miombo woodlands. He found that germination occurred readily and rapidly after sustained rain. The taproot grew strongly and produced laterals which were colonized by EM fungi before emergence. The mycorrhizas appeared to be the same as those found on the mother tree, and it seemed likely that the early mycorrhizal development drew on carbon from the mature tree.

Magingo & Dick (2001) pointed out that seed of *miombo* trees can be difficult to obtain and tends to have very short periods of viability. They have successfully propagated *B. spiciformis*, *Pterocarpus angolensis* and two other common *miombo* species by leafy stem cuttings in simple non-mist propagators suitable for the rural tropics (the design of the ITE non-mist propagator is shown in Leakey & Newton, 1994, p.243). Magingo & Dick suggest that this procedure makes it possible to develop clones of genetically superior specimens for use in agroforestry or reforestation programmes. Earlier work with *Faidherbia albida* in Burkina Faso had found that cuttings produced several taproots and survived drought less well than seedlings, which developed a single taproot (Ouedraogo, 1993), but Magingo and Dick found that *B. spiciformis* cuttings developed good healthy root systems with a single taproot. They further suggest that coppicing good quality stock trees at 1.3 m should produce a good crop of shoots suitable for use as leafy cuttings before the beginning of the rainy season, and stress the importance of synchronizing plant production with the seasons. Chidumayo *et al* (1996) argue that management of existing stands of *Brachystegia* and *Julbernardia* species by coppicing and selective thinning may

be a better option than establishing plantations, since coppice regrowth is relatively fast, while the above-ground development of seedlings of these species is very slow for the first ten years.

The EM status of *B. spiciformis* was attested by Hogberg and Pearce (1986) and Alexander (1989), and confirmed in Burkina Faso by Sanon *et al* (1997), who also surprisingly observed AM on baiting plants. Not all EM fungi associated with adult trees will form mycorrhizas with nursery-raised seedlings (Munyanziza, 1994; Mason *et al*, 1983); it would be interesting to establish whether leafy cuttings taken from adult stock trees would accept inocula of fungal species which produce good crops of edible fungi under adult trees, and whether they would then retain this association until maturity.

*Pterocarpus angolensis* is one of the most valuable African timber trees, with a range of provenances of differing drought, fire and frost tolerances, and with different growth forms of interest in timber production (Frost, 1996). It is a nodulating legume and forms arbuscular mycorrhizas (Hogberg, 1990; Munyanziza & Oldeman, 1996). Sprent (2001) notes that African *Pterocarpus* species nodulate readily with Brazilian rhizobial strains. Munyanziza (1994) found most nodules on the taproot. He reported that this species has been over-exploited and is now protected, and he considered it suitable and attractive for agroforestry and the reclamation of degraded sites. He and two Indian colleagues state that mycorrhizal plants have greater tolerance to transplant shock, and they consider mycorrhizal inoculation to be indispensable for tree planting on disturbed sites (Munyanziza *et al*, 1997). He observed natural regeneration in Tanzania; the fruits are lightweight and winged, so dispersal by wind occurs, but they are not attractive to animals

or birds. The fruits ripen and drop towards the end of the dry season; pod breakdown occurs during the first rains, followed by slow corrosion of the seed coat, and the seed is ready to germinate early in the rainy season of the following year. Munyanziza noted that seeds germinating at this time produced a taproot averaging 47.5 cm in length, while the taproots of seeds germinating late in the rainy season only averaged 7.6 cm in length. In order to reproduce this vital synchronization of seed germination and onset of the rains he recommended harvesting mature pods from the tree, hot-wire scarification and shallow sowing with adequate water at the beginning of the rainy season. This method accelerates the natural dormancy-breaking process and achieves correct seasonal timing while simplifying seed-handling.

Rapid development of a deep taproot is a key strategy for *P. angolensis*, but makes nursery production difficult. Munyanziza and Oldeman (1996) reported a shoot: root ratio of 0.25 in miombo seedlings growing unimpeded. In miombo woodland the natural strategy of *P. angolensis* seedlings is to grow a small annual shoot each year while developing a large and efficient root system with a very deep, swollen taproot. During the dry seasons the shoot dies back or is likely to be burned off by bushfire. After 8-10 years, when adequate resources have been stored in the root, the plant puts up a shoot of 2-3 m in a single rainy season. This is often tall enough to survive bushfire, and the young tree will then grow normally and fairly quickly (Celander, 1983). If grown in the nursery with continued irrigation, shoot dieback does not occur, but the seedling completes its shoot and leaf development in three and a half months and the apical shoot then becomes dormant. Seedlings grown in closed containers develop coiled roots very quickly; those grown in

open-bottomed containers become anchored in the soil below, and need to be cut free. One or two root prunings in the first two months, just before outplanting, can be tolerated as the taproot still has the capacity to reiterate, but the seedling will be vulnerable to dry season stress (Munyanziza & Oldeman, 1996). Munyanziza (1994) considers direct sowing in the field a good option if rainfall is assured and regular; otherwise he recommends nursery raising in inoculated soil, one or two root prunings only, and outplanting at two to two and a half months with the prospect of at least 2 months rain. Magingo and Dick (2001) report successful striking of leafy stem cuttings, also in inoculated soil.

*Tamarindus indica* grows in low altitude woodland, wooded grassland and along rivers. It is the favourite indigenous fruit tree among the Sukuma people of NW Tanzania. Its fruit is frequently traded, and it also produces fodder, firewood and tool handles. It germinates well after direct sowing and can also be propagated from leafy stem cuttings. It is regarded as a prime candidate for domestication (Buwalda *et al*, 1997; Milimo, 1994). Bâ *et al* (2000) found it to be highly mycorrhizal-dependent with *Glomus aggregatum*.

*Uapaca kirkiana* has been described and studied by Ngulube *et al* (1995, 1997, 1998). The species has a wide natural range in tropical Africa, from 2-21° S and almost coast to coast, typically on well-drained escarpments between 500 and 2000 m.a.s.l. with infertile acid sandy or gravelly soils, and unimodal rainfall averaging 500-1400 mm annually. There is strong demand for its nutritious whole fruits, and these are also used by a growing juice and wine-making industry. Its wood is used as fuel, charcoal, posts and handles. It is under evaluation for agroforestry and afforestation, and provenance trials leading to a selective

breeding programme are recommended. Seed viability is short, but germination is rapid (2-7 weeks). *U. kirkiana* is dioecious. Soil from established stands was used by Ngulube and associates in germination trials, and they state that successful establishment depends partly on mycorrhizal inoculation. This had been strongly suggested by an earlier trial (Mwamba et al, 1992) which compared the poor field-performance of direct-seeded or container-grown seedlings with that of naturally germinated seedlings dug out complete with rootball from a wild *U. kirkiana* stand. The container-grown seedlings were in sterilized soil from an established *U. kirkiana* stand. Only the naturally germinated seedlings were mycorrhizal, apparently with *Amanita* aff. *rubescens* (Pers. Fr.) S.F.Gray, and their survival and growth were very much better than those of the seedlings which had had the other treatments.

The mycorrhizal relationships of *U. kirkiana* are intriguing. As noted in Section 1.1.2.2., in the natural fire-regeneration sequence, it establishes in an AM community of grasses and scattered trees. It then develops an ectomycorrhiza and enables EM *Brachystegia* and *Julbernardia* species to establish themselves under its canopy. Observations of another member of the *Uapaca* genus by Thoen and Bâ (1989) in Senegal suggest a possible explanation. Adult individuals of *U. guineensis* bear both EM and AM. Primary infection by AM followed later by EM colonization is known to occur in several genera which are unrelated but are all small-seeded, as is *U. guineensis*. EMF require higher carbohydrate levels than AMF, so young *Uapaca* seedlings growing in isolation may be able to support AM but not EM development. When they mature they are open to colonization by airborne EMF spores and develop substantial EM networks which can then foster exclusively EM tree species.

**Summary Table (a) Some tree species suitable for dryland recovery or protection**

Species	Uses	Importance for anti-desertification	Mycorrhizal information	Growth conditions/climatic range
<i>Acacia tortilis</i>	fodder (pods) charcoal shelter belts	wide distribution on desert margins thorny saplings resist premature browsing	associated with 12 AMF species in Rift Valley responsive to unselected mycorrhizal inocula from several sources in Kenya assumed to be mycodependent in S Tunisia indigenous AMF out-competed <i>Glomus mosseae</i> in Senegal, but were ineffective	tolerates high temperatures & drought prefers light, well-drained soil intolerant of heavy clays & flooding
<i>Acacia nilotica</i>	fodder(pods/inflorescence) forage timber poles/handles	good for agroforestry - roots proliferate below crop rooting zone successful in Shinyanga	highly mycorrhizal mycodependent with exotic <i>Glomus intraradices</i> AM-rhizobial inoculation increased plant growth	tolerates high temperatures tolerates heavy clays & flooding
<i>Acacia senegal</i> var. <i>senegal</i>	gum arabic	dominant in wide sub-saharan belt extensive surface & deep root system already widely used for anti-desertification important cash earner	found with <i>Glomus fasciculatum</i> & <i>Gigaspora margarita</i> at 34 m depth	tolerates hot, dry, rocky/sandy sites
<i>Faidherbia albida</i>	dry season fodder/pods	beneficial on farmed Sahelian parkland	selection of high performance strains of Indigenous AMF recommended in Senegal <i>Glomus aggregatum</i> & <i>Glomus manihotis</i> +rock phosphate enhanced plant growth	wide rainfall range intolerant of competition from grasses during establishment
<i>Acacia holosericea</i>		quick-growing, adapts to most soils, but sensitive to long droughts	inoculation with <i>Glomus mosseae</i> increased Nodulation & shoot weight dramatically (local AMF strains may optimize N-fixation & plant growth) <i>G. aggregatum</i> most common AMF partner in monospecific Burkina Faso plantation	fairly high rainfall requirement tolerates saline & water-logged soils
<i>Acacia mangium</i>	firewood	used for rehabilitation of difficult sites	<i>G. aggregatum</i> most common AMF partner in monospecific Burkina Faso plantation one provenance formed EM and grew well	suitable for difficult sites
<i>Acacia saligna</i>	forage firewood	used for dune stabilization		(intolerant of cold and salinity)
<i>Acacia salicina</i>	firewood shelter	very drought-tolerant vigorous suckering		
<i>Adansonia digitata</i> (baobab)	fruit fodder medicinal	forms islands of fertility (very slow-growing)	only marginally mycorrhizal-dependent with <i>Glomus aggregatum</i> and <i>Glomus intraradices</i>	very wide rainfall range prefers sandy soils overlying loam but tolerates poorly drained soils
<i>Argania spinosa</i>	browse edible oil	low rainfall requirement tolerates most soil types		tolerates arid conditions in most soils except drifting sands & water-logging

<i>Azadirachta indica</i>	fodder timber oil	drought resistant & fast growing thrives on poor soils popular for shelterbelts successful in rotational woodlots in Shinyanga endangered by pests in Sahel widely used in land reclamation	highly myco-dependent with <i>G. aggregatum</i> inoculation with <i>G. fasciculatum</i> +phosphate-solubilizing bacteria beneficial in India	tolerates extreme temperatures & drought thrives in poor semi-arid soils but responds well to 450-600 mm rainfall
<i>Calliandra calothyrsus</i>	fodder firewood		very responsive in biomass & P uptake to inoculation with a range of cultured AMF	
<i>Cordeauxia edulis</i>	nuts fodder dye	endemic in arid SE Somalia & Ogaden can survive 2 years without rain incipient fruits go dormant in drought & mature quickly when rain comes slow top growth but can fruit in 3-4 years		85-200 mm rainfall compacted sand and sandy loam intolerant of water-logging tolerates slight salinity
<i>Melia volkensii</i>	timber firewood fruit fodder	grows from stem cuttings & suckers (difficult to germinate) fast growing		native in semi-arid E. Africa needs 450 mm rainfall minimum well-drained soil
<i>Moringa oleifera</i>	oil protein-rich pods & leaves water-purifier	propagates easily by seed or cuttings very fast-growing	mycorrhizal dependency under investigation	400-1200 mm rainfall grows up to 1200-1500 m a.s.l. frost-intolerant optimum temperature range 15-35 °C
<i>Moringa stenopetala</i>	protein-rich pods & leaves water-purifier shelter	more drought-resistant than <i>M. oleifera</i> popular in W. Ethiopia		native in E. Africa rainfall 250-1400 mm well-drained soils fruits up to 1800 m
<i>Parkia biglobosa</i> <i>P. clappertonia</i> <i>P. filicoidea</i>	protein-rich pods/seeds	valued in parkland farming systems fast-growing good survival in drought (non-nodulating) adapted to harsh conditions (can become a weed)	moderately myco-dependent with sahelian isolate of <i>Glomus aggregatum</i>	370-890 rainfall
<i>Prosopis juliflora</i>	fodder firewood		inoculation with <i>G. fasciculatum</i> improved plant growth in Jodhpur, where indigenous AMF were ineffective	marginal arid/semi-arid good for soil amelioration less good for intercropping
<i>Vitellaria paradoxa</i> (shea tree)	oil fruit pharmaceuticals	well-known agroforestry tree from Sahel to Uganda (slow-growing) (endangered by parasite in Sahel)		500-1200 mm rainfall

<i>Ziziphus mauritiana</i> (Jujube)	fruit nectar fodder fuel hedging	widely grown in Sahel, E Africa & India fast-maturing suitable rootstock grows widely in drier areas	highly myco-dependent with <i>G. aggregatum</i> <i>G. fasciculatum</i> appeared to improve resistance of plant to pathogens	low/medium altitude intolerant of extreme temperatures will grow at lower end of semi-arid gradient but more vigorous & productive at higher end tolerates some water-logging any soil, including saline ones
--	--	--	---	---

**(b) Some miombo species appropriate for former dry forest areas:**

Species	Uses	Importance for anti-desertification	Mycorrhizal information	Growth conditions/climatic range
<i>Brachystegia spiciformis</i>	charcoal nectar edible fungi valuable timber	germinates readily under mature individuals propagation by leafy stem cuttings can produce improved cultivars can be propagated by leafy stem cuttings nodulates readily with known rhizobia (fast-growing taproot a problem in nursery)	EM, but AM observed on bait plants late-stage EMP will not necessarily form mycorrhizas with nursery seedlings mycorrhizal plants have greater tolerance to transplant shock	intolerant of waterlogging, often found on ridges  range of provenances with differing drought-, fire- & frost tolerances
<i>Tamarindus indica</i>	fruit fodder firewood handles	favourite in degraded area of N W Tanzania prime candidate for domestication direct sowing successful can be propagated by leafy stem cuttings wide natural range key species in natural regeneration sequence strong demand for products	highly myco-dependent with <i>G. aggregatum</i>	low altitude & along rivers
<i>Uapaca kirkiana</i>	fruit charcoal firewood posts/handles		AM > EM succession uninoculated seedlings grow poorly	well-drained escarpments 500-2000 m.a.s.l. infertile acid sandy/gravelly soils



#### 5.4. AM fungal partners

Much of the evidence associating AMF with beneficial effects on plants does not identify the fungal species involved, and suggests that a mixture rather than a single AMF species is likely to be present, although one cannot even begin to speculate on the relations between the various fungal species, or on their relative effectiveness as symbionts. However, a few species have been repeatedly identified and may merit special attention, though it must always be remembered that different isolates can show considerable divergence and local ones may be most effective in their own environment.

*Glomus aggregatum* was the commonest AMF found on the exotics *Acacia holoserica* and *Acacia mangium* on two mature monospecific plantations in Burkina Faso by Bâ *et al* (1996). It was also identified with *Faidherbia albida* in the Sahelian region of Senegal (Dalpé *et al*, 2000). Bâ *et al* (2000) tested its effectiveness as an inoculant with thirteen fruit trees in Senegal, and found it beneficial to some but not others; *Ziziphus mauritiana* benefited most, followed by *Tamarindus indica*, *Parkia biglobosa* and others in descending order. It is considered native in eroded rangeland in S.E. Spain, and proved a more effective inoculant than *Glomus mosseae* when tested on indigenous grasses and leguminous shrubs (Roldán-Fajardo, 1994). It is common in coastal barrier dunes from New Jersey to Virginia (Koske, 1987, and under grasses in Minnesota, particularly at the sandy end of a sand-sandy loam soil gradient (Johnson *et al*, 1992). It was the most frequent AMF throughout a latitudinal gradient of *Artemisia tridentata*/*Atriplex gardneri* shrub steppe in SW Wyoming (Allen *et al*, 1995). It was common under fescue sod in Kentucky, but declined when ploughed and sown with crabgrass or pearl millet (Hendrix *et al*, 1995). (This may be a

consideration where agroforestry with scattered trees and intercrops such as millet and sorghum is practised).

*Glomus fasciculatum* was found associated with *Faidherbia albida* near the surface and at 34 m deep (Dalpé *et al*, 2000). An early investigation of depth of root symbiont occurrence under *Prosopis globulosa* in the Californian Sonoran desert found an AMF thought to be *G. fasciculatum* just above the water table at a depth of about 4.5 m (Virginia *et al*, 1986). It was shown to be beneficial in terms of plant growth and nutrient uptake with *Azadirachta indica* (Neem), particularly when co-inoculated with phosphate-solubilizing bacteria (Kalavathi *et al*, 2000). Mathur and Vyas (1995) report that it is one of the most commonly occurring AMF in arid and semi-arid regions, and that it appears to increase the defences of plants against pathogens by stimulating the production of defensive enzymes. In SE Spain it proved to be a more effective inoculant for the indigenous *Spartium junceum* than a *Scutellospora* species isolated from the rhizosphere of that shrub (Herrera *et al*, 1993). It has been found in a low rainfall area of N Dakota (Rives *et al*, 1980), in semi-arid Wyoming (Allen *et al*, 1995), western Colorado (Moorman & Reeves, 1979), Nebraska, (Allen, 1982), and present but not dominant in sand-sandy loam in Minnesota (Johnson *et al*, 1992). It was found at all depths tested, down to 2.2 m, in Kansas (Zajicek *et al*, 1986), and mainly in the top 30 cm but down to 1 m depth in a semi-arid mid-elevation sage community in south west USA (Schwab & Reeves, 1981). It is associated with young *Citrus* in California and Florida (Nemec *et al*, 1981), and is frequent in New South Wales (Hayman & Stovold, 1979). In contrast with *G. aggregatum*, it became more common in Kentucky when fescue sod was cultivated with pearl millet (Hendrix *et al*, 1995).

*Glomus intraradices* occurs on almost every continent. It survives high temperatures, is effective on *Citrus* and common under rotated crops, features which suggest possible suitability for agroforestry applications in hot climates.

The genus *Gigaspora* is particularly associated with hot countries such as Libya, and with sandy soils. *Gigaspora margarita* enhanced the growth and nutrient uptake of *Tectona grandis* in a pot experiment in Coimbatore, India, using local sandy loam of pH 8 (Sugavanam *et al*, 1998). It was also found at 34 m depth under *Faidherbia albida* at a Sahelian site in Senegal (Bâ & Guissou, 1996), suggesting a possible role with deep-rooting dryland trees.

## 5.5. Discussion

The tree species described above are major resources and their conservation, development and exploitation have an importance transcending any possible role in anti-desertification measures. Many are fairly quick-growing and most are widely known, valued and used, though not necessarily propagated, by local people. However, *Adansonia digitata* (baobab) and *Vitellaria paradoxa* (shea) are slow-growing and though common and revered now, they may be at long-term risk unless their conservation and propagation comes to be seen as a regional or national responsibility. If that were the case it would be important for extension services to be able to provide either good quality seedlings ready inoculated with inoculum harvested from the rhizosphere of healthy specimens of the same species.

It is important that any attempt to introduce new methods or ideas should be seen as helping local people achieve objectives they already perceive as valid and useful. Where there are indigenous fruit or other tree species of recognized economic value in an area suffering from some degree of desertification, a collaborative project for the production of inoculated seedlings of the species of interest would be a good starting point. With some species, provenances or individuals can differ considerably in their characteristics, including the quality and quantity of their products. In that case domestication and selective improvement could be implemented through a project involving the vegetative propagation of material taken from superior specimens identified by local people. Vegetative propagation has been shown to produce good root development in some species (Magingo, pers. comm.), though not in *Faidherbia albida* (Ouedraogo, 1993), and is compatible with mycorrhizal inoculation, so a combined project involving the production of young trees and an experiment in mycorrhizal inoculation might be valuable and popular.

Knowledge of the mycorrhizal dependency of potentially useful trees is very patchy. Where no mycorrhizal information is included in the descriptions above, it is usually because no relevant information has been found in the course of a fairly extensive survey of the literature. Even where some evidence of dependency or otherwise exists, it will relate to particular soils and inocula, and often to particular (sometimes unstated) nutrient levels. It may also be affected by the presence or absence of other microsymbionts or of pathogens; one of the benefits of mycorrhizal colonization mentioned earlier was protection against pathogens, but clearly a pot experiment using sterilized substrate with or without cultured mycorrhizal inoculum would not take account of this possible benefit.

Many dryland tree species develop a long taproot very quickly, which makes their management in the nursery difficult. Root pruning is a standard procedure but may well compromise the ability of the plant to establish contact with groundwater before the onset of the dry season. Munyanziza suggested that one or at most two very early root prunings followed by early outplanting can be tolerated by some species and may be the best compromise. REDMED are experimenting with long tubular plant containers (cf. Section 4.3.3.), and these may well prove very valuable in the right circumstances, but inappropriate to farmers whose main tool is the mattock. The answer in some cases may be either direct sowing, of pregerminated seed where possible, with inoculum added to the planting hole, or very short and very carefully (seasonally) timed nursery production followed by outplanting before the taproot reaches the bottom of the container. The difficulty with these alternatives is the variability in the onset of the rainy season. The optimum procedure may be different for different species, and this whole question would repay investigation.

## 6. Conclusions

Semi-arid ecosystems are adapted to variable periods of severe stress, and striking recovery has been achieved in some fairly recently degraded drylands without any special mycorrhizal measures. In such cases, symbiotic soil microorganisms presumably remained present in a dormant state or continued to be active in pockets of good natural vegetation. In contrast, where desertification has been very extensive or longstanding, populations of symbiotic soil microorganisms are likely to be too depleted to be effective. In such cases, reclamation will be difficult, but providing sufficient topsoil remains, the simultaneous reintroduction of suitable plants and soil symbionts offers a possible recovery strategy.

### 6.1. General discussion

Mycorrhizal symbiosis is an unequal relationship in that the fungi are totally dependent on plants for their energy supply, whereas for most plants the mycorrhiza only supplements and extends the range of their nutrient- and water-absorbing root system. Indeed, experiments with AM plants show that in nutrient-rich, well-irrigated conditions some mycorrhizal plants grow less quickly than non-mycorrhizal ones (Hetrick *et al*, 1990).

However, in nutrient-poor soils, particularly P-deficient ones, mycorrhizal symbiosis can bring substantial benefits to plant survival, growth or reproductive capacity. In fact, examples have been given where in particular conditions the symbiosis appears to be essential to the plant, and investigations of a range of tree species have determined varying degrees of mycorrhizal dependency. The studies at Menzel Habib, described in Section

4.3.1., identified *Acacia tortilis* ssp. *raddiana* as a keystone species, loss of which constituted the crossing of a 'threshold of irreversibility'. The irreversibility of this descent to a worse level of desertification resides in the virtual disappearance of the acacias from the landscape and from the soil seed bank, plus the consequent loss of the symbiotic partners on which the acacias had depended: *Rhizobium* and AMFs. This does not mean that *Rhizobium* and AMFs have disappeared entirely, but that they are in general much depleted and that in particular the most compatible and beneficial strains or species of microbes, if present at all, are very sparse. The result is that if a stray acacia germinated or were planted, it would either not encounter any suitable AMF (and rhizobial) partners at all, or would only encounter quite inadequate numbers and be colonized to a very small degree. This would not give the plant sufficient support and, consequently, it would probably not survive the first drought. If it did, it would be stunted and unlikely ever to grow to its normal size.

This view is supported by the evidence from Somalia and Australia, reported in Section 3.5.3.1., which suggests strongly that degraded dryland suffers a sharp drop in mycorrhizal infectivity, and that though cultivated land may retain a considerable population of mycorrhizal fungi, the species composition of that population is changed. In such circumstances the improvement of vegetation, mycorrhizal functioning and soil structure need to be addressed together.

**Mycorrhizal functioning.** Research carried out in SE Spain, described in Section 4.3.3., found that AMF present in land which had been used for marginal agriculture, probably for

centuries, and had then been abandoned about 50 years ago, achieved high levels of colonization of *Anthyllis cytisoides*, considered to be natural to the area, both in the field and in greenhouse tests. However, these AMF were ineffective in improving plant growth, whereas augmentation of the soil with an inoculum of *Glomus intraradices* did improve growth. It was inferred that the AMF species composition had changed due to agriculture, and would no longer support an extensive revegetation programme. For that, it would be necessary to introduce inoculum from an outside source (Requena *et al*, 1996). Further investigation suggested that the key factor might be the presence or absence of a particular native *Rhizobium*. Thus, the original AMF could still be present but be ineffective as symbionts for woody plants because other key microorganisms had been lost.

*The role of agroforestry in conservation.* The minimization of soil erosion is a prime objective of anti-desertification measures, and is usually, though not always, accompanied by the urgent need to restore higher levels of productivity. The outplanting of mycorrhizally inoculated trees or shrubs could satisfy the dual aim of simultaneously raising productivity and improving the microbial life and the aggregation of the soil.

The resilience of tropical savanna makes it a model for man-made solutions to the problem of sustainable use of drylands: parkland or agroforestry provide shelter from scorching and desiccating conditions, havens and often “islands of fertility” for plants and soil microorganisms, as well as valuable tree products.



The successful parkland or agroforestry developments cited in Section 4.2 have built on an existing framework of scattered trees or shrubs surviving from previous woodland or savanna. These species survived because they are valued for their products and because they are adapted to the local environment. They are likely to harbour useful levels of appropriate AMF, and in many cases they regenerate naturally. Farmers are accustomed to working round them. It would be wise to consider these first – whether they merit more extensive planting and whether improved cultivars can be developed. The next step might be to consider and discuss with local farmers what other woody species might be suitable and of interest, and how they might be incorporated into local land-use systems. A selection of fruit, timber or multipurpose species suitable for a range of semi-arid conditions was profiled in Section 5. Some of these will be indigenous to the region; others will be well-known and popular exotics.

***Mycorrhizal inoculation.*** It is very important that tree seedlings destined for outplanting on semi-arid sites are mycorrhizally inoculated at early nursery stage. In many semi-arid regions this may appear to be a problem, but it is really an opportunity to use local resources to the best advantage. It was noted above that surviving trees or shrubs are likely to harbour pockets of appropriate mycorrhizal fungi. Sampling and culturing these fungal resources and then using them as inoculum in local nurseries contributes to their conservation and to ecosystem restoration (Shepherd *et al*, 1996).

The low-cost method of AM inoculation developed in Kenya by Munro *et al* (1999) is strongly advocated, and its implementation is indeed the central recommendation of the

present review. Munro's approach is consistent with the notion that in savanna or former woodland areas that have suffered a degree of degradation, if the original mycorrhizal fungi are still present at all, they will be found in the rhizosphere of woody plants. They will not necessarily be in high concentrations, but since AMF are fairly promiscuous they can be multiplied by trap-pot culture with fast-growing mycotrophic host plants. The approach also meets the stipulations defined by Requena *et al* (1997) in their work in SE Spain, that local isolates of AMF should be used, together with non-sterile soil likely to contain any other symbiotic microorganisms that the host plant might be harbouring, such as PGPRs, and possibly *Rhizobium* if the host is a legume. As Munro *et al* point out, the procedure is simple, and could be easily applied in village tree nurseries. It also has the merit of being educational in that it raises awareness of natural soil processes and how to work with them. However, it should be noted that it would not have been effective in Almeria if *Anthyllis* individuals that had recolonized the former agricultural site had been used as the source from which to gather inoculum; they had evidently regained a foothold but were apparently not benefitting from their mycorrhizal association. To fulfil their potential they needed inoculum of a species not present on the site (though it might have been present under *Anthyllis* growing on a nearby hillside). Care is needed in selecting donor trees for inoculum harvesting; in an area where desertification has been recent and where healthy pockets of natural vegetation appear to have survived unscathed, suitable donors should be easily accessible, but where there has been either widespread or longstanding disturbance it may be necessary to go further afield in search of starter inoculum. The Menzel Habib researchers refer to a reference ecosystem. This was presumably an area known to them where the vegetation was relatively unscathed and was considered comparable to the pre-

disturbance state of the area they were attempting to improve. The acacias there would be a promising source of wild inoculum.

*Problems of deep roots.* Deep-rootedness is a fundamental characteristic of most of the woody species profiled in Chapter 5. The astonishing speed with which very young seedlings put down a long taproot was highlighted by Munyanziza (cf. Section 5.3.3), who described the dilemma which this posed in the tree nursery; the common practice of root-pruning attacks the survival mechanism evolved by these species. This problem comes within the terms of reference of the REDMED project described in Section 4.3.3). Munyanziza's solutions were either very limited and early root-pruning, quickly followed by outplanting, or direct sowing into the field. Direct sowing is not necessarily incompatible with inoculation; a plug of inoculum prepared by the trap-pot method could be inserted into the soil surface and the tree seeds sown into it. This might give satisfactory infection if the soil of the site was generally deficient in fungal propagules, but would probably fail if it was an agricultural site with an undesirable AMF species composition, as those species would be likely to outcompete the inoculum. An alternative might be germinating and growing the seedlings in nursery containers for a month or so, and outplanting before the taproot reached the bottom of the container. The REDMED research project will investigate long containers and direct seeding of long-taprooted dryland species, and their results and recommendations will be eagerly awaited.

*Climate change and human factors.* When remedial or preventative measures against desertification are being considered, it is important to distinguish between environmental

deterioration arising solely from excessive human pressure and deterioration in which the human damage is compounded by adverse climate change. It is widely predicted that global warming will cause significant climate shifts, and in particular that northern Africa and the Mediterranean region may become drier. It has been convincingly argued that savanna ecosystems are inherently transitional, and have an inbuilt resilience which absorbs and cushions climatic fluctuations, even extended droughts of 20-50 years, but if the climate shift is not a fluctuation but a long-term trend, it is clear that restoration (cf. Section 4.3.1.) might not be an attainable objective, and rehabilitation or reallocation programmes might need to be tailored to the harsher climatic conditions which are predicted. Such programmes would probably include the introduction of useful plant species with greater drought tolerance than those currently or previously dominant in the area.

Most desertification situations occur on marginal dryland where there is heavy pressure from an often growing population needing to gain a livelihood from their land, and in this case any remedial measures need to improve short- as well as longer-term yield of food, fodder, fuel or other marketable products. But this is not always so, and SE Spain was quoted in Section 4.3.3. as an example of the movement of population away from marginal agriculture and into an intensively exploited coastal strip. This poses a very serious threat to the watertable and the future economy of the whole region. In these circumstances, policies for the desertified hinterland are likely to be based increasingly on the overriding need for protection from further erosion, in order to maximize infiltration and the recharging of aquifers and minimize runoff and evaporation. A protective rather than a productive vegetation will be required. The establishment of clumps of indigenous woody

legumes, or species such as *Tetraclinis articulata* or *Argania spinosa* which are native to drier but otherwise climatically similar areas of the Maghreb, surrounded by vegetatively propagated *Stipa tenacissima*, all mycorrhizally inoculated, would appear appropriate, and would be an interesting experimental project on a site liable to damaging runoff.

## **6.2. How strong is the evidence?**

The evidence for desertification as a major threat is compelling. Natural semi-arid ecosystems are resilient but also vulnerable, and excessive human pressure has undermined or endangered the productivity of very large areas. Water is a key resource, and where a high percentage of an area's water resources passes rapidly through without bringing benefit, and often doing damage, the system is clearly dysfunctional.

Since mycorrhizal fungi are obligate symbionts, and fungal propagules have a limited lifespan, deforestation, loss of plant cover and erosion inevitably lead, in the long term, to mycodeficient soils, as reported from Spain, Ethiopia, Chile and USA (Requena *et al*, 1996; Roldán *et al*, 1997; Michelsen & Rosendahl, 1989; Ovalle *et al*, 1995; Reeves *et al*, 1979; Allen, 1989). The deficiency may be an overall depletion of fungal propagules, or, as in some cultivated land, a changed fungal population (cf. Section 3.5.3.1.), but in either case the evidence seems quite clear that trees outplanted into these conditions are most unlikely to encounter adequate populations of appropriate mycorrhizal symbionts.

It has been shown that dryland plants are normally mycorrhizal, that AMF are highly adapted to arid conditions, and that mycodependency tends to rise along a gradient of

increasing aridity and nutrient-poverty. The coarse-rootedness characteristic of legumes and C<sub>4</sub> grasses has been shown to be a contributory factor to mycodependency, so it is reasonable to infer that land suffering from extensive and long-term desertification will be mycodeficient, and consequently trees planted there without mycorrhizal inoculation will be unlikely to thrive. This evidence is strong enough to base inoculation programmes on. On the other hand, the evidence from areas such as Machakos and Kondoa shows that land which has suffered serious but recent degradation and has retained pockets of natural vegetation can be surprisingly resilient; vegetation can recover and trees can be outplanted without special inoculation programmes. This is not to say that inoculation in the nursery will not benefit them, but it is important to distinguish situations where inoculation may be essential for good survival and growth in the field, from situations where it is not.

Land which has been cultivated is a special case. It has been shown that cultivation can change the species balance of AMF, and that this may be disadvantageous to outplanted trees and shrubs. For practical purposes it may be wise to inoculate with appropriate AMF seedlings destined for outplanting on such land, as a precautionary measure, but site-specific tests would be required before a need for inoculation could be proven.

There is strong evidence that AMF isolates can vary considerably, and adapt to local conditions, and that this can affect their effectiveness as symbionts. The presumption is that local isolates, collected from the wild, may well be particularly appropriate due to local adaptation, but this is clearly no more than a reasonable initial presumption, based on a few

known instances, together with general evolutionary theory. It needs to be tested, and in any particular situation local isolates may prove ineffective or worse.

Certain AMF species have been identified at great depths. There are four separate reports of *Glomus fasciculatum* at depths down to 34 m, three of them fairly old but one recent. Taken together, they constitute very strong evidence, and experimental inoculation of deep-rooting tree species with this fungus is justified, but whether this will set up an effective and continuing mycorrhizal development at depth is speculative; the idea warrants testing, but would be difficult to monitor.

Mycorrhizal information on particular woody species is extremely scanty, as can be seen from Section 5. In some cases, no mycorrhizal reference has been found. Where there is information, it is mostly from a single trial. Such information is valuable as a pointer, but needs to be tested as widely as possible before too much weight is attached to it. The limitations of the information available on the mycorrhizal dependency of tree species of interest were discussed in Section 5.5.

The question of the synergy of AMF and other soil microorganisms is a good example. There is good evidence that combined inoculation with AMF and phosphate-solubilizing bacteria can be beneficial when applied together with rock phosphate in an alkaline low-P soil (cf. 3.4.). The evidence is strong enough to warrant further trials in comparable circumstances, but until this is done it will not be known whether the effect depends on

particular local conditions, or a particular combination of AMF and bacterial species which may or may not be widespread.

### **6.3. Recommendations to development agencies and NGOs**

**Awareness:** The last two decades have seen the publication of a large body of research, much of which points to the importance of mycorrhizal symbiosis, and soil with inoculum potential is sometimes explicitly mentioned in reports of experimental work on indigenous tree species of potential economic value in semi-arid countries. But it is not clear that this awareness on the part of the researchers has as yet done much to influence general practice. Stockpiled soil, agricultural soil and soil collected from bare fallow all appear as tree nursery substrate. Such soils are likely either to be mycorrhizally impoverished or to contain a predominance of AMF propagules of unsuitable types, which will be ineffective as symbiotic partners for the tree seedlings they will colonize.

Many soils do not make good nursery substrate, and consequently soilless composts which encourage better root development are widely used in developed countries. If this practice spreads in semi-arid developing countries it could result in the production of healthy seedlings which would grow well in good conditions but lack the mycorrhizal dimension which would assist their establishment in more severe outplanting environments. It is quite possible to combine the benefits of both systems by using a potting mixture which is mainly soilless but includes a small proportion of mycorrhizal soil as inoculum, and which has a restricted P content. It would be desirable to put the case for this to development organizations.



**Validation of simple procedures at local level:** There is widespread appreciation of the value and importance of woody plants as protection and as a productive resource and much interest in the potential of both indigenous and introduced species. A number of species of interest have been described in the present review; it would be useful to identify local situations, initially in East Africa or the Sahel, where there was an interest in or demand for a particular species and where small collaborative projects could be set up to produce a supply of the desired seedlings while at the same time testing the simple mycorrhizal procedure advocated by Munro *et al* (1999), described in 4.3.4. and elaborated on in the Protocol set out in Appendix 1. One such situation is already known to exist in the Dodoma region of Tanzania, where there is an NGO interest in *Moringa oleifera* and *Moringa stenopetala*. Results from a number of such trials would help to establish how well the procedure performed as a response to a range of desertification situations, and whether more sophisticated manipulations were indicated in the more stressful environments.

**Combined domestication/mycorrhization.** The Sukuma region of Tanzania has been identified as an area suffering serious desertification. *Tamarindus indica* has been noted as the favourite indigenous fruit tree among the Sukuma people and has been proposed for domestication. This type of situation might offer scope for testing simple mycorrhizal inoculation procedures within a programme for the production and distribution of improved cultivars. Vegetative propagation might be particularly appropriate in such cases, and Magingo & Dick (2001) advocate the use of leafy stem cuttings taken from good quality

coppiced stock trees and grown in mycorrhizal soil in simple non-mist propagators (cf. Section 5.3).

**More sophisticated procedures.** (a) The deep-rooting strategy of many key dryland species raises the question whether only certain AMF species or isolates are adapted to accompany the plant roots to deep water tables. Both *Glomus fasciculatum* and *Gigaspora margarita* have been found at 34 m depth associated with the roots of *Faidherbia albida* in Senegal. It would be interesting to test whether pure inoculum of Senegalese isolates of these fungal species, used either alone or in combination with local mixed inocula, appeared to confer extra benefit on deep rooting seedlings in drought-stressed areas. A possible approach is outlined in Appendix 2.

(b) Results from a number of trials of the Munro procedure might be expected to show a variety of outcomes, ranging from successful to ineffective. Inoculum from successful trials could be studied and multiplied at forestry establishments, and tested at sites where the local wild inoculum had proved ineffective.

## References :

- Alexander, I.J. (1989) Systematics and ecology of ectomycorrhizal legumes. In: Stirton, C.H. & Zaricchi, J.L. (eds.) *Advances in Legume Biology*. Monographs of Systematic Botany, Missouri Botanic Garden **29**, 607-624.
- Allen, E.B. (1991) Temporal and Spatial Organization of Desert Plant Communities. In: Skujins, J. (ed.) *Semiarid Lands and Deserts: Soil Resources and Reclamation*.
- Allen, E.B., Allen, M.F., Helm, D.J., Trappe, J.M., Molina, R. & Rincon, E. (1995) Patterns and regulation of mycorrhizal plant and fungal diversity. *Plant and Soil* **170**, 47-62.
- Allen, M.F. (1982) Influence of vesicular-arbuscular mycorrhizae on water movement through *Bouteloua gracilis* (H.B.K.) Lag ex Steud. *New Phytologist* **91**, 191-196.
- Allen, M.F. (1989) Mycorrhizae and rehabilitation of disturbed arid soils: processes and practices. *Arid Soil Research and Rehabilitation*, **3**, 229-241.
- Allen, M.F. (1991) *The Ecology of Mycorrhizae*. CUP.
- Allen, E.B., Allen, M.F., Helm, D.J., Trappe, J., Molina, R. & Rincon, E. (1995) Patterns and regulation of mycorrhizal plant and fungal diversity. *Plant and Soil* **170**, 47-62.
- Anon. (1994) Notes and Records. *African Journal of Ecology* **32**, 327-330.
- Anon. (1993) Notes and Records. *African Journal of Ecology* **31**, 84-86.
- Aronson, J., Floret, C., Le Floc'h, E., Ovalle, C. & Pontanier, R. (1993a) Restoration and Rehabilitation of Degraded Ecosystems in Arid and Semi-Arid Lands. 1. A View from the South. *Restoration Ecology* **1**, 8-17.
- Aronson, J., Floret, C., Le Floc'h, E., Ovalle, C. & Pontanier, R. (1993b) Restoration and Rehabilitation of Degraded Ecosystems in Arid and Semi-Arid Lands. II. Case Studies in Southern Tunisia, Central Chile and Northern Cameroon. *Restoration Ecology* **1**, 168-187.
- Arya, S., Toky, O.P., Harris, P.J.C. & Harris, S.M. (1992) *Prosopis cineraria* and *Azadirachta indica*. A surprising association. *Agroforestry Today*, Jul-Sep 1992, 9-10.
- Asimi, S., Gianinazzi-Pearson, V. & Gianinazzi, S. (1980) Influence of increasing soil phosphorus levels on interactions between vesicular-arbuscular mycorrhizae and *Rhizobium* in soybeans. *Canadian Journal of Botany* **58**, 2200-2205.
- Audru, J., Labonne, M., Guérin, A. & Bilha, A. (1993) *Acacia nilotica*. Its value as fodder and its exploitation by the Afar of Djibouti. *Bois et Forêts des Tropiques* **235**, p.70.
- Ayoub, A.T. (1998) Extent, severity and causative factors of land degradation in the Sudan. *Journal of Arid Environments* **38**, 397-409.
- Azcón, R. (1987) Germination and hyphal growth of *Glomus mossae* *in vitro*: effects of rhizosphere bacteria and cell-free culture media. *Soil Biology and Biochemistry* **19**, 417-419.
- Azcón, R. (1993) Growth and nutrition of nodulated mycorrhizal and non-mycorrhizal *Hedysarum coronarium* as a result of treatment with fractions from a plant growth-promoting rhizobacteria. *Soil Biology and Biochemistry* **25**(8), 1037-1042.
- Azcón, R., Barea, J.M. & Hayman, D.S. (1976) Utilization of rock phosphate in alkaline soils by plants inoculated with mycorrhizal fungi and phosphate-solubilizing

- bacteria. *Soil Biology and Biochemistry* **8**, 135-138.
- Azcón, R., Rubio, R. & Barea, J.M. (1991) Selective interactions between different species of mycorrhizal fungi and *Rhizobium meloti* strains, and their effect on growth, N<sub>2</sub>-fixation and nutrition of *Medicago sativa* L. *New Phytologist* **117**, 399-404.
- Bâ, A.M., Dalpé, Y. & Guissou, T. (1996) Les glomales d'*Acacia holosericea* et d'*Acacia mangium*. *Bois et Forêts des Tropiques* **250(4)**, 5-18.
- Bâ, A.M., Plenchette, C., Danthu, P., Duponnois, R. & Guissou, T. (2000) Functional compatibility of two arbuscular mycorrhizae with thirteen fruit trees in Senegal. *Agroforestry Systems* **50**, 95-105.
- Bâ, A.M. & Guissou, T. (1996) Rock phosphate and vesicular-arbuscular mycorrhiza effects on growth and nutrient uptake of *Faidherbia albida* (Del.) seedlings in an alkaline soil. *Agroforestry Systems* **34**, 129-137.
- Bagnoud, N., Schmithusen, F. & Sorg, J-P. (1995) The shea tree and locust bean tree parklands in southern Mali. *Bois et Forêts des Tropiques* **244**, 22-23.
- Barea, J.M., Andrade, G., Bianciotto, V., Dowling, D., Lohrke, S., Bonfante, P., O'Gara, F. & Azcón-Aguilar, C. (1998) Impact on Arbuscular Mycorrhizal Formation of *Pseudomonas* Strains Used as Inoculants for Biocontrol of Soil-Borne Fungal Pathogens. *Applied and Environmental Microbiology* **64(6)**, 2304-2307.
- Barea, J.M., Azcón-Aguilar, C. & Azcón, R. (1987) Vesicular arbuscular mycorrhizas improve both symbiotic N<sub>2</sub> fixation and N uptake from soil as assessed with a <sup>15</sup>N technique under field conditions. *New Phytologist* **106**, 717-725.
- Barea, J.M., Azcón-Aguilar, C. & Azcón, R. (1997) Interactions between mycorrhizal fungi and rhizosphere micro-organisms within the context of sustainable soil-plant systems. In: Gange, A.C. & Brown, V.K. (eds.) *Multitrophic Interactions in Terrestrial Systems*. Blackwell Scientific, Oxford.
- Barnes, R.D. (2001) The African Acacias – A thorny subject. *Southern African Forestry Journal* **190**, 9-17.
- Barrow, E.G.C. (1991) Building on local knowledge. The challenge of agroforestry for pastoral areas. *Agroforestry Today* (Oct-Dec), 4-7.
- Baylis, G.T.S. (1975) The magnolioid mycorrhiza and mycotrophy in root systems derived from it. In: *Endomycorrhizas*. Sanders, F.E., Mosse, B. & Tinker, P.B., p.373. Academic Press, London.
- Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R. & Mwonga, S.M. (1989) The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* **26**, 1005-1024.
- Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M. & Ali, A.R. (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology* **30**, 143-155.
- Bethlenfalvay, G.J., Dakessian, S. & Pacovsky, R.S. (1984) Mycorrhizae in a southern Californian desert: ecological implications. *Canadian Journal of Botany*, **62**, 519-524.
- Bever, J.D. & Morton, J. (1999) Heritable variation and mechanisms of inheritance of spore shape within a population of *Scutellospora pellucida*, an arbuscular mycorrhizal fungus. *American Journal of Botany* **86(9)**, 1209-1216.
- Bianciotto, V., Bandi, C., Minerdi, D., Sironi, M., Tichy, H.V. & Bonfante, P. (1996) An Obligately Endosymbiotic mycorrhizal Fungus Itself Harbours Obligately Intracellular Bacteria. *Applied and Environmental Microbiology* **62(8)**, 3005-3010

- Blomley, T. (1994) Indigenous agroforestry. *Melia volkensii* in Kenya. *Agroforestry Today* (Oct-Dec), 10-11.
- Boaler, S.B. (1966) Ecology of a *miombo* site, Lupa North Forest Reserve, Tanzania. 2. Plant communities and seasonal variation in the vegetation. *Journal of Ecology* **54**, 465-479.
- Boaler, S.B. & Sciwale, K.C. (1966) Ecology of a *miombo* site, Lupa North Forest Reserve, Tanzania. 3. Effects on the vegetation of local cultivation practices. *Journal of Ecology* **54**, 577-587.
- Boerner, R.E.J. (1990) Role of mycorrhizal fungus origin in growth and nutrient uptake by *Geranium robertianum*. *American Journal of Botany* **77**(4), 483-489.
- Boffa, J.-M., Yaméogo, G., Nikiéma, P. & Taonda, J.-B. (1996) What future for the shea tree? *Agroforestry Today* (Oct-Dec), 5-9.
- Bounejmame, M., Beale, P.E. & Robson, A.D. (1992) Annual Medicago Species in Morocco. 1. Species and their Abundance. *Australian Journal of Agricultural Research* **43**, 739-74.
- Bourliere, F. & Hadley, M. (1983) Present-day Savannas; an Overview. In: *Ecosystems of the World, Vol. 13, Tropical Savannas*. Bourliere, F. (ed.) chap.1. Elsevier, Amsterdam.
- Braunberger, P.G., Abbott, L.K. & Robson, A.D. (1994) The effect of rain in the dry-season on the formation of vesicular-arbuscular mycorrhizas in the growing season of annual clover-based pastures. *New Phytologist* **127**, 107-114.
- Brock, T.D., Madigan, M.T., Martinko, J.M. & Parker, J. (1994) *Biology of Microorganisms*. Prentice-Hall International (UK), London.
- Brundett, M.C. (1991) Mycorrhizas in Natural Ecosystems. *Advances in Ecological Research* **21**, 171-313.
- Brundett, M.C. & Abbott, L.K. (1991) Roots of Jarrah forest plants. I. Mycorrhizal associations of shrubs and herbaceous plants. *Australian Journal of Botany* **39**, 445-457.
- Brundett, M.C. & Abbott, L.K. (1994) Mycorrhizal fungus propagules in the jarrah forest. 1. Seasonal studies of inoculum levels. *New Phytologist* **127**, 539-546.
- Brundett, M.C. & Kendrick, B. (1990) The roots and mycorrhizas of herbaceous woodland plants. II. Structural aspects of morphology. *New Phytologist* **114**, 469-479.
- Brundett, M.C., Piché, Y. & Peterson, R.L. (1985) A developmental study of the early stages in vesicular-arbuscular mycorrhizal formation. *Canadian Journal of Botany* **63**, 184-194.
- Bryla, D.R. & Duniway, J.M. (1997/a) Growth, phosphorus uptake, and water relations of safflower and wheat infected with an arbuscular mycorrhizal fungus. *New Phytologist* **136**, 581-590.
- Bryla, D.R. & Duniway, J.M. (1997/b) Water uptake by safflower and wheat roots infected with arbuscular mycorrhizal fungi. *New Phytologist* **136**, 591-601.
- Budi, S.W., van Tuinen, D., Martinotti, G. & Gianinazzi, S. (1999) Isolation from the *Sorghum bicolor* Mycorrhizosphere of a Bacterium Compatible with Arbuscular Mycorrhiza development and Antagonistic towards Soilborne Fungal Pathogens. *Applied and Environmental Microbiology* **65**(11), 5148-5150.
- Busso, C.A. (1997) Towards an increased and sustainable production in semi-arid rangelands of central Argentina: two decades of research. *Journal of Arid Environments* **36**, 197-210.

- Buwalda, A.O., Otsyina, R., Filson, G. & Machado, V.S. (1997) Indigenous miombo fruit trees - health and wealth for the Sukuma people. *Agroforestry Today* (Jul-Sep), 23-25.
- Caldwell, M.M. & Richards, J.H. (1989) Hydraulic lift; water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* **79**, 1-5.
- Campbell, B., Frost, P. & Byron, N. (1996) Miombo woodlands and their use; overview and key issues. In: *The Miombo in Transition: Woodlands and Welfare in Africa*. CIFOR, Bogor, Indonesia, 1-10.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**, 583-595.
- Carpenter, A.T. & Allen, M.F. (1988) Responses of *Hedysarum boreale* Nutt. to mycorrhizas and *Rhizobium*: plant and soil nutrient changes in a disturbed shrub-steppe. *New Phytologist* **109**, 125-132.
- Celander, N. (1983) *Miombo woodlands in Africa – distribution, ecology and patterns of land use*. Working Paper 16, Swedish University of Agricultural Sciences, Uppsala.
- Chidumayo, E., Gambiza, J. & Grundy, I. (1996) Managing miombo woodlands. In: Campbell, B. (ed.) *The miombo in transition: woodlands and welfare in Africa*. CIFOR, Bogor, Indonesia.
- Christiansson, C., Kikula, I.S. & Ostberg, W. (1991) Man-Land Interactions in Semiarid Tanzania: A Multidisciplinary Research Program. *Ambio* **20**, 357-361.
- Clark, S.C. (1996) Mediterranean Ecology and an Ecological Synthesis of the Field Sites. In: Brandt, C.J. & Thornes, J.B., *Mediterranean Desertification and Land Use*, pp.271-300. John Wiley, Chichester.
- Cornet, F. & Diem, H.G. (1982) Etude comparative de l'efficacité des souches de *Rhizobium* d'*Acacia* isolées de sols du Sénégal et effet de la double symbiose *Rhizobium-Glomus mosseae* sur la croissance de *Acacia holosericea* et *A. raddiana*. *Bois et Forêts des Tropiques* **198(4)**, 3-15.
- Cossalter, C. (1986) Introducing Australian acacias in dry, tropical Africa. In: Turnbull, J.W. (ed.) *Australian Acacias in Developing Countries*. ACIAR, Canberra, 118-122.
- Daft, M.J. & El Giahmi, A.A. (1976) Studies on nodulated and mycorrhizal peanuts. *Annals of Applied Biology* **83**, 273-276.
- Dalpe, Y., Diop, T.A., Plenchette, C. & Gueye, M. (2000) Glomales species associated with surface and deep rhizosphere of *Faidherbia albida* in Senegal. *Mycorrhiza* **10**, 125-129.
- Daniels, B.A. & Trappe, J.M. (1980) Factors affecting spore germination of the vesicular-arbuscular mycorrhizal fungus, *Glomus epigaeus*. *Mycologia*, **72**, 457-471.
- Dawson, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* **95**, 565-574.
- De la Cruz, R.E., Manalo, M.Q., Aggangan, N.S. & Tambalo, J.D. (1988) Growth of three legume trees inoculated with VA mycorrhizal fungi and *Rhizobium*. *Plant and Soil* **108**, 111-115.
- De Soyza, G., Whitford, W.G., Herrick, J.E., Van Zee, J.W. & Havstad, K.M. (1998) Early warning indicators of desertification: examples of tests in the Chihuahuan Desert. *Journal of Arid Environments* **39**, 101-112.

- di Castri, F. (1981) Mediterranean-type Shrublands of the World. In : *Ecosystems of the World, Vol. 11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L. (eds.) chap.1. Elsevier, Amsterdam.
- Dick-Peddie, W.A. (1991) Semiarid and Arid Lands; a World-wide Scope. In: *Semiarid Lands and Deserts: Soil Resource and Reclamation*. Skujins, J. (ed.) pp.2-32. Marcel Dekker, N.Y.
- Diop, T.A., Gueye, M., Dreyfus, B.L., Plenchette, C. & Strullu, D.G. (1994) Indigenous Arbuscular Mycorrhizal Fungi Associated with *Acacia albida* Del. in Different Areas of Senegal. *Applied and Environmental Microbiology* **60** (9), 3433-3436.
- Diouf, M. & Grouzis, M. (1996) Natural Distribution of *Acacia tortilis* (Forssk.) Hayne subsp. *raddiana* (Savi) Brenan in Senegal: Ecological Determinism *International Tree Crops Journal* **9**, 69-75.
- Dougill, A. & Trodd, N. (1999) Monitoring and modelling open savannas using multisource information: analyses of Kalahari studies. *Global Ecology and Biogeography*, **8**, 211-221.
- Duponnois, R. & Ba, A.M. (1999) Growth stimulation of *Acacia mangium* Willd. by *Pisolithus* sp. in some Senegalese soils. *Forest Ecology and Management* **119**, 209-215.
- Duponnois, R. & Garbaye, J. (1990) Some mechanisms involved in growth stimulation of ectomycorrhizal fungi by bacteria. *Canadian Journal of Botany* **68**, 2148-2152.
- Dupuy, N.C. & Dreyfus B.L. (1992) *Bradyrhizobium* Populations occur in Deep Soil under the Leguminous Tree *Acacia albida*. *Applied and Environmental Microbiology* **58**(8), 2415-2419.
- El-Lakany, M.H. (1986) Use of Australian acacias in North Africa. In: Turnbull, J.W. (ed.) *Australian Acacias in Developing Countries*. ACIAR, Canberra. 116-117.
- Ewing, M.A. (1999) Annual Pasture Legumes: A Vital Component Stabilizing and Rehabilitating Low-Rainfall Mediterranean Ecosystems. *Arid Soil Research and Rehabilitation* **13**, 327-342.
- Fenner, M. (1980) Some measurements on the water relations of baobab trees. *Biotropica* **12**, 205-209.
- Fitter, A.H. & Garbaye, J. (1994) Interactions between mycorrhizal fungi and other soil Organisms. *Plant and Soil* **159**, 123-132.
- Folkard, G. & Sutherland, J. (1996) *Moringa oleifera*: a tree and a litany of potential. *Agroforestry Today* Jul-Sep 1996, 5-8.
- Fox, J.E.D. (1986) Potential of Australian acacias from arid and semi-arid zones. in: Turnbull, J.W. (ed.) *Australian Acacias in Developing Countries*. ACIAR, Canberra. 17-28.
- Francis, R. & Read, D.J. (1994) The contributions of mycorrhizal fungi to the determination of plant community structure. *Plant and Soil* **159**, 11-25.
- Freckman, D.W. & Virginia, R.A. (1989) Plant-feeding nematodes in deep-rooting desert ecosystems. *Ecology* **70**(6), 1665-1678.
- Fredrickson, E., Havstad, K.M., Estell, R. & Hyder, P. (1998) Perspectives on desertification: south-western United States. *Journal of Arid Environments* **39**, 191-207.
- Frey-Klett, P., Churin, J-L., Pierrat, J-C. & Garbaye, J. (1999) Dose effect in the dual inoculation of an ectomycorrhizal fungus and a mycorrhiza helper bacterium in two

- forest nurseries. *Soil Biology and Biochemistry* **31**(11), 1555-1562.
- Frey-Klett, P., Pierrat, J.C. & Garbaye, J. (1997) Location and Survival of Mycorrhiza Helper *Pseudomonas fluorescens* during Establishment of Ectomycorrhizal Symbiosis between *Laccaria bicolor* and Douglas Fir. *Applied and Environmental Microbiology* **63**(1), 139-144.
- Fries, F. (1991) Management of Natural Forests in the Semiarid Areas of Africa. *Ambio* **20**(8), 395-400.
- Friese, C.F. & Allen, M.F. (1991) The spread of VA mycorrhizal fungal hyphae in the soil; inoculum types and external hyphal architecture. *Mycologia*, **83**(4), 409-418.
- Frost, P. (1996) The ecology of miombo woodlands. In: Campbell, B. (ed.) *The miombo in transition: woodlands and welfare in Africa*. CIFOR, Bogor, Indonesia.
- Garbaye, J. (1994) Tansley review No.76: Helper bacteria: a new dimension to the mycorrhizal symbiosis. *New Phytologist* **128**, 197-210.
- Gianinazzi-Pearson, V., Gianinazzi, S. & Trouvelot, A. (1985) Evaluation of the infectivity and effectiveness of indigenous vesicular-arbuscular fungal populations in some agricultural soils in Burgundy. *Canadian Journal of Botany* **63**, 1521-1524.
- Gibson, F. & Deacon, J.W. (1990) Establishment of ectomycorrhizas in aseptic culture: effects of glucose, nitrogen and phosphorus in relation to successions. *Mycological Research* **94**, 166-172.
- Gillison, A.N. (1983) Tropical Savannas of Australia and the South West Pacific. In: *Ecosystems of the World, vol. 13, Tropical Savannas*. Bourliere, F. (ed.), chap.9. Elsevier, Amsterdam.
- Gillon, D. (1983) The Fire Problem in Tropical Savannas. In: *Ecosystems of the World, Vol. 13, Tropical Savannas*. Bourliere, F. (ed.), chap.30. Elsevier, Amsterdam.
- Giovannetti, M., Azzolini, D. & Citerne, A.S. (1999) Anastomosis Formation and Protoplasmic Exchange in Arbuscular Mycorrhizal Fungi. *Applied and Environmental Microbiology* **65**(12), 5571-5575.
- Gould, A.B. & Liberta, A.E. (1981) Effects of topsoil storage during surface mining on viability of vesicular-arbuscular mycorrhiza. *Mycologia*, **73**, 914-922.
- Graham, J.H. & Eissenstat, D.M. (1994) Host genotype and the formation and function of VA mycorrhizae. *Plant and Soil* **159**, 179-185.
- Green, J.J., Vallejo, R., Serrano, I., Martins-Loucao, M.A., Hatzistathis, A., Barea, J.M., Cortina, J. & Watson, C.A. (1999) Restoration of degraded ecosystems in Mediterranean regions (REDMED). In: *Grasslands and woody plants in Europe*, 281-286. Papanastasis, V.P., Frame, J. and Natis, A.S. (eds.). Thessaloniki: HERPAS.
- Grime, J.P., Mackey, J.M.L., Hillier, S.H. & Read, D.J. (1987) Floristic diversity in a model system using experimental microcosms. *Nature* **328**, 420-422.
- Guevara, J.C., Stasi, C.R., Wuilloud, C.F., & Estevez, O.R. (1999) Effects of fire on rangeland vegetation in south-western Mendoza plains (Argentina): composition, frequency, biomass, productivity and carrying capacity. *Journal of Arid Environments* **41**, 27-35.
- Guidot, A., Lumini, E., Debaud, J.-C. & Marmeisse, R. (1999) The Nuclear Ribosomal DNA Intergenic Spacer as a Target Sequence To Study Intraspecific Diversity of the Ectomycorrhizal Basidiomycete *Hebeloma cilindrosporum* Directly on *Pinus* root Systems. *Applied and Environmental Microbiology* **65**(3), 903-909.
- Haas, J.H. & Krikun, J. (1985) Efficacy of endomycorrhizal-fungus isolates and



- inoculum quantities required for growth response. *New Phytologist* **100**, 613-621.
- Habte, M. & Manjunath, A. (1987) Soil Solution Phosphorus Status and Mycorrhizal Dependency in *Leucaena leucocephala*. *Applied and Environmental Microbiology* **53**(4), 797-801.
- Habte, M., Muruleedhara, B.N. & Ikawa, H. (1993) Response of Neem (*Azadirachta indica*) to Soil P Concentration and Mycorrhizal Colonization. *Arid Soil Research and Rehabilitation* **7**, 327-333.
- Habte, M. & Turk, D. (1991) Response of two species of *Cassia* and *Gliricidia sepium* to vesicular-arbuscular mycorrhizal infection. *Communications in Soil Science and Plant Analysis* **22**, 1861-1872.
- Hanes, T.L. (1981) California Chaparral. In: *Ecosystems of the World, Vol. 11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L. (eds.) pp. 139-170. Elsevier, Amsterdam.
- Harley, J.L. & Smith, S.E. (1983) *Mycorrhizal Symbiosis*. Academic Press, London.
- Hayman, D.S. & Stovold, G.E. (1979) Spore Populations and Infectivity of Vesicular Arbuscular Mycorrhizal fungi in New South Wales. *Australian Journal of Botany* **27**, 227-233.
- Hendricks, D.M. (1991) Genesis and Classification of Arid Region Soils. In: *Semiarid Lands and Deserts: Soil Resource and Reclamation*. Skujins, J. (ed.) pp. 39-79. Marcel Dekker, N.Y.
- Hendrix, J.W., Guo, B.Z. & An, Z-Q. (1995) Divergence of mycorrhizal fungal communities in crop production systems. *Plant and Soil* **170**, 131-140.
- Heppell, K.B., Shumway, D.L. & Koide, R.T. (1998) The effect of mycorrhizal infection of *Abutilon theophrasti* on competitiveness of offspring. *Functional Ecology* **12**, 171-175.
- Herrera, M.A., Salamanca, C.P. & Barea, J.M. (1993) Inoculation of Woody Legumes with Selected AMF and Rhizobia to Recover Desertified Mediterranean Ecosystems. *Applied and Environmental Microbiology* **59**, 129-133.
- Hetrick, B.A.D., Kitt, D.G. & Wilson, G.T. (1988) Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie species. *Canadian Journal of Botany* **66**, 1376-1380.
- Hetrick, B.A.D., Wilson, G.W.T. & Todd, T.C. (1990) Differential responses of C<sub>3</sub> and C<sub>4</sub> grasses to mycorrhizal symbiosis, phosphorus fertilization, and soil microorganisms. *Canadian Journal of Botany* **68**, 461-467.
- Hill, J., Hostert, P., Tsiourlis, G., Kasapidis, P., Udelhoven, Th. & Diemer, C. (1998) Monitoring 20 years of increased grazing impact on the Greek island of Crete with earth observation satellites. *Journal of Arid Environments* **39**, 165-178.
- Hogberg, P. (1986) Soil nutrient availability, root symbioses and tree species composition in tropical Africa: a review. *Journal of Tropical Ecology* **2**: 359-372.
- Hogberg, P. (1990) <sup>15</sup>N natural abundance as a possible marker of the ectomycorrhizal habit of trees in mixed African woodlands. *New Phytologist* **115**, 483-486.
- Hogberg, P. & Pearce, G.D. (1986) Mycorrhizas in Zambian trees in relation to host taxonomy, vegetation type and successional patterns. *Journal of Ecology* **74**, 775-785.
- Hopkins, B. (1965) Observations on savanna burning in the Olokemeji Forest Reserve, Nigeria. *Journal of Applied Ecology* **2**, 367-381.
- Hopkins, B. (1983) Successional Processes. In: *Ecosystems of the World, vol. 13, Tropical*

- Savannas*. Bourliere, F. (ed.), chap.29. Elsevier, Amsterdam.
- Hutchinson, C.F. (1996) The Sahelian desertification debate: a view from the American south-west. *Journal of Arid Environments* **33**, 519-524.
- Ibrahim, M.A., Campbell, W.F., Rupp, L.A. & Allen, E.B. (1990) Effects of Mycorrhizae on Sorghum growth, Photosynthesis, and Stomatal Conductance under Drought Conditions. *Arid Soil Research and Rehabilitation* **4**, 99-107.
- Ichire, O. (1993) Trees for food and fodder production in dryland Nigeria. *Agroforestry Today* (Jan-Mar), 12-13.
- Ingleby, K., Diagne, O., Deans, J.D., Lindley, D.K., Neyra, M. & Ducousso M. (1997) Distribution of roots, arbuscular mycorrhizal colonization and spores around fast-growing tree species in Senegal. *Forest Ecology and Management* **90**, 19-27.
- Isichei, A.O. & Sanford, W.W. (1980) Nitrogen loss by burning from Nigerian grassland ecosystems. In: *Nitrogen Cycling in West African Ecosystems*. Rosswall, T. (ed.). SCOPE/UNEP International Nitrogen Unit, Royal Swedish Academy of Sciences, Stockholm.
- Jacobson, K.M. (1997) Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in an arid grassland. *Journal of Arid Environments* **35**, 59-75.
- Jaenicke, H. (1999) *Good Tree Nursery Practices; Practical Guidelines for Research Nurseries*. ICRAF, Nairobi, p.13.
- Jahn, S.A.A (1991) The Traditional Domestication of a Multipurpose Tree *Moringa stenopetala* (Bak.f) Cuf. in the Ethiopian Rift Valley. *Ambio* **20(6)**, 244-247.
- Jasper, D.A. (1992) Soil disturbance in native ecosystems – the decline and recovery of infectivity of VA mycorrhizal fungi. In: *Mycorrhizas in Ecosystems*. Read, D.J., Lewis, D.H., Fitter, A.H. & Alexander, I.J. (eds.). CAB International, Wallingford, UK. pp.151-155.
- Jasper, D.A., Abbott, L.K. & Robson, A.D. (1989) Hyphae of a vesicular-arbuscular mycorrhizal fungus maintain infectivity in dry soil, except when the soil is disturbed. *New Phytologist* **112**, 101-107.
- Jasper, D.A., Abbott, L.K. & Robson, A.D. (1991) The effect of soil disturbance on vesicular-arbuscular mycorrhizal fungi in soils from different vegetation types. *New Phytologist* **118**, 471-476.
- Jasper, D.A., Abbott, L.K. & Robson, A.D. (1993) The survival of infective hyphae of vesicular-arbuscular mycorrhizal fungi in dry soil: an interaction with sporulation. *New Phytologist* **124**, 473-479.
- Jeffers, J.N.R. & Boaler, S.B. (1966) Ecology of a *miombo* site, Lupa North Forest Reserve, Tanzania. I. Weather and plant growth, 1962-64. *Journal of Ecology* **54**, 447-463.
- Jeffries, P. & Barea, J.M. (1994) Biogeochemical cycling and arbuscular mycorrhizas in the sustainability of plant-soil systems. In: *Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems*. Gianinazzi S. & Schuepp, H. (eds.) Birkhauser Verlag, Basel/Switzerland, 101-115.
- Jenkins, M.B., Virginia, R.A. & Jarrel, W.M. (1988) Depth Distribution and Seasonal Populations of Mesquite-Nodulating Rhizobia in Warm Desert Ecosystems. *Soil Science Society of America Journal* **52**, 1644-1650.
- Joffre, R. & Rambal, S. (1993) How tree cover influences the water balance of

- mediterranean rangelands. *Ecology* **74**(2), 570-582.
- Johnson, N.C., Graham, J.H. & Smith, F.A. (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist* **135**, 575-585.
- Johnson, N.C., Tilman, D. & Wedin, D. (1992) Plant and soil controls on mycorrhizal fungal communities. *Ecology* **73**(6), 2034-2042.
- Jones, M.D., Durall, D.M. & Tinker, P.B. (1998) A comparison of arbuscular and ectomycorrhizal *Eucalyptus coccifera*: growth response, phosphorus uptake and external hyphal production. *New Phytologist* **140**, 125-134.
- Kalavathi, B.P., Santhanakrishnan, P. & Divya, M.P. (2000) Effect of VA-mycorrhizal fungus and phosphorus solubilizing bacterium in Neem. *Indian Forester* (Jan), 67-70.
- Kennenni, L. (1991) Geography and phytosociology of *Acacia tortilis* in the Sudan. *African Journal of Ecology* **29**, 1-10.
- Kessy, B.S. (1986) Growth of Australian Acacias in Tanzania. In: Turnbull, J.W. (ed.) *Australian Acacias in Developing Countries*. ACIAR, Canberra. 123-125.
- Khan, S.N. & Uniyal, K. (1999) Growth response of two forest trees to VAM and *Rhizobium* inoculations. *Indian Forester*, Nov. 1999, 1125-1127.
- Kidundo, M. (1997) *Melia volkensii* – propagating the tree of knowledge. *Agroforestry Today*, Apr-Jun 1997, 21-22.
- Kiers, E.T., Lovelock, C.E., Krueger, E.L. & Herre, E.A. (2000) Differential effects of tropical arbuscular fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity. *Ecology Letters* **3**, 106-113.
- Kikula, I.S. (1999) Lessons from Twenty-five Years of Conservation and Seven Years of Research in the Kondoa Highlands of Central Tanzania. *Ambio* **28**, 444-449.
- Koske, R.E. (1975) *Endogone* spores in Australian sand dunes. *Canadian Journal of Botany* **53**, 668-672.
- Koske, R.E. (1987) Distribution of VA Mycorrhizal Fungi along a Latitudinal Temperature Gradient. *Mycologia* **79**(1), 55-68.
- Kovacik, D.A., St. John, T.V. & Dyer, M.I. (1984) Lack of vesicular-arbuscular mycorrhizal inoculum in a ponderosa pine forest. *Ecology* **65** (6): 1755-1759.
- Khresat, S.A., Rawajfih, Z. & Mohammad, M. (1998) Land degradation in north-western Jordan: causes and processes. *Journal of Arid Environments* **39**, 623-629.
- Kumar, P.P., Reddy, S.R. & Reddy S.M. (2000) Mycorrhizal dependency of some agroforestry tree species. *Indian Forester*, Apr, 397-402.
- Kummerow, J. (1981) Structure of Roots and Root Systems. In: *Ecosystems of the World, Vol. 11, Mediterranean-type Shrubland*. di Castri, F., Goodall, D.W. and Specht, R.L. (eds.), pp 269-288. Elsevier, Amsterdam.
- Lale, N.E.S. (1998) Neem in the Conventional Lake Chad Basin area and the threat of Oriental yellow scale insect (*Aonidiella orientalis* Newstead) (Homoptera: Diaspididae) *Journal of Arid Environments* **40**(2), 191-197.
- Lambert, D.H., Cole, H.Jr. & Baker, D.E. (1980) Adaptation of vesicular- arbuscular mycorrhizae to edaphic factors. *New Phytologist* **85**, 513-520.
- Lamien, N., Sidibe, A. & Bayala, J. (1996) The joy of cooking – recipes for the success of the shea tree. *Agroforestry Today* Oct-Dec 1996, 10-11.
- Lapeyrie, F.F., & Chilvers, G.A. (1985) An endomycorrhiza-ectomycorrhiza succession associated with enhanced growth of *Eucalyptus dumosa* seedlings planted in a calcareous soil. *New Phytologist* **100**, 93-104.

- Lawson, G.W., Jeník, J. & Armstrong-Mensah, K.O. (1968) A study of a vegetation catena in Guinea savanna at Mole Game Reserve (Ghana). *Journal of Ecology* **56**, 505-522.
- Lawton, R.M. (1978) A study of the dynamic ecology of Zambian vegetation. *Journal of Ecology* **66**, 175-198.
- Leakey, R.R.B. & Newton, A.C. (eds.) (1994) *Tropical trees; the potential for domestication and the rebuilding of forest resources*. ITE symposium no. 29. HMSO, London.
- Le Floc'h, E., Neffati, M., Chaieb, M., Floret, C. & Pontanier, R. (1999) Rehabilitation Experiment at Menzel Habib, Southern Tunisia. *Arid Soil Research and Rehabilitation* **13**, 357-368.
- Le Houérou, H.N. (1981) Impact of Man and his Animals on Mediterranean Vegetation. In: *Ecosystems of the World, Vol. 11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L. (eds.) chap. 25. Elsevier, Amsterdam.
- Le Houérou, H.N. (1996) Climate change, drought and desertification. *Journal of Arid Environments* **34**, 133-185.
- Le Houérou H.N. (2000) Utilization of Fodder Trees and Shrubs in the Arid and Semiarid Zones of West Asia and North Africa. *Arid Soil Research and Rehabilitation* **14**, 101-135.
- Lesueur, D., Tassin, J., Enorilac, M-P., Sarrailh, J-M. & Peltier, R. (1996) La symbiose *Calliandra calothyrsus*-Rhizobium. *Bois et Forêts des Tropiques* **248(2)**, 43-57.
- Lewis, J.D. & Koide, R.T. (1990) Phosphorus supply, mycorrhizal infection and plant offspring vigour. *Functional Ecology* **4**, 695-702.
- Litav, M. (1965) Mycorrhizal association in dwarf shrub species growing in soft cretaceous rocks. *Journal of Ecology* **53**, 147-151.
- Lodoen, D. (1998) Prospering through diversity. *Agroforestry Today* (Apr-June), 16-17.
- McGee, P. (1986) Mycorrhizal associations of plant species in a semiarid community. *Australian Journal of Botany* **34**: 585-593.
- McGee, P.A. (1989) Variation in propagule numbers of vesicular-arbuscular mycorrhizal fungi in a semi-arid soil. *Mycological Research* **92(1)**, 28-33.
- McGee, P.A., Pattinson, G.S., Heath, R.A., Newman, C.A. & Allen, S.J. (1997) Survival of propagules of arbuscular mycorrhizal fungi in soils in eastern Australia used to grow cotton. *New Phytologist* **135**, 773-780.
- Maghembe, J.A. (1994) Out of the forest. Indigenous fruit trees in southern Africa. *Agroforestry Today*, Apr-Jun, 4-5.
- Maghembe, J.A. (1994) Domestication potential of indigenous fruit trees of the miombo woodlands of southern Africa. In: *Tropical trees; the potential for domestication and the rebuilding of forest resources*. Leakey, R.R.B. & Newton, A.C. (eds.). ITE Symposium no.29, 220-229. HMSO, London.
- Magingo, F.S.S. & Dick, J. McP. (2001) Propagation of two woodland trees by leafy stem cuttings obtained from seedlings. *Agroforestry Systems* **51**, 49-51.
- Malloch, D.W., Pirozynski, K.A. & Raven, P.H. (1980) Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (A Review). *Proceedings of the National Academy of Science, USA* **77(4)**, 2113-2118.
- Manjunath, A., Bagyaraj, D.J. & Gopala Gowda, H.S. (1984) Dual inoculation with VA mycorrhiza and *Rhizobium* is beneficial to *Leucaena*. *Plant and Soil* **78**, 445-448.

- Marschner, H. & Dell, B. (1994) Nutrient uptake in mycorrhizal symbiosis. *Plant and Soil* **159**, 89-102.
- Mason, P.A., Wilson, J. & Last, F.T. (1983) The concept of succession in relation to the spread of sheathing mycorrhizal fungi on inoculated tree seedlings growing in unsterile soils. *Plant and Soil* **71**, 247-256.
- Mason, P.A. & Wilson, J. (1994) Harnessing symbiotic associations: vesicular-arbuscular mycorrhizas. In: *Tropical trees: the potential for domestication and the rebuilding of forest resources*, 165-175. Leakey R.R.B. & Newton, A.C. (eds.) ITE Symposium No.29, HMSO.
- Mathur, N. & Vyas, A. (1995) Changes in Isozyme patterns of Peroxidase and Polyphenol Oxidase by VAM fung in Roots of *Ziziphus* species. *Journal of Plant Physiology* **145**, 498-500.
- Mathur, N. & Vyas, A. (1999) Improved Biomass Production, Nutrient Uptake and Establishment of *In Vitro* Raised *Ziziphus mauritiana* by VA Mycorrhiza. *Journal of Plant Physiology* **155**, 129-132.
- Mayer, F.A. & Stelz, E. (1993) *Moringa stenopetala* provides food and low-cost water purification. *Agroforestry Today* Jan-Mar 1993, 16-17.
- Mayo, K., Davis, R.E. & Motta, J. (1986) Stimulation of germination of spores of *Glomus versiforme* by spore-associated bacteria. *Mycologia* **78**, 426-431.
- Mbegu, A.C. (n/d) *The HADO Project; What, Where, Why, How?* JAMAA General Agencies. P.O.Box 58059, Tanzania.
- Meigs, P. (1953) World distribution of arid and semi-arid homoclimates. In: *Review of Research of Arid Zone Hydrology, Arid Zone Programme I*, UNESCO, Paris, pp.203-209.
- Mgeni, A.S.M. (1992) Farm and Community Forestry (Village Afforestation) Program in Tanzania; Can it go Beyond Lipservice? *Ambio* **21**, 426-430.
- Michelsen, A. (1992) Mycorrhiza and root nodulation in tree seedlings from five nurseries in Ethiopia and Somalia. *Forest Ecology and Management* **48**, 335-344.
- Michelsen, A. (1993) Growth improvement of Ethiopian acacias by addition of vesicular arbuscular mycorrhizal fungi or roots of native plants to non-sterile nursery soil. *Forest Ecology and Management* **59**, 193-206.
- Michelsen, A. & Rosendahl, S. (1989) Propagule density of VA-mycorrhizal fungi in semi-arid bushland in Somalia. *Agriculture, Ecosystems and Environment* **29**, 295-301.
- Michelsen, A. & Sprent, J.I. (1994) The influence of vesicular-arbuscular mycorrhizal fungi on the nitrogen fixation of nursery-grown Ethiopian acacias estimated by the <sup>15</sup>N natural abundance method. *Plant and Soil* **160**, 249-257.
- Milimo, P.B., Dick, J.McP. & Munro, R.C. (1994) Domestication of trees in semi-arid East Africa: the current situation. In: Leakey, R.R.B., and Newton, A.C. (eds.) *Tropical trees; the potential for domestication and the rebuilding of forest resources*. (ITE Symposium no. 29, ECTF Symposium no.1). HMSO.
- Miller, R.M. (1979) Some occurrences of VAM in natural and disturbed ecosystems of the Red Desert of Wyoming. *Canadian Journal of Botany* **57**, 619-623.
- Miller, R.M., Carnes, B.A. & Moorman, T.B. (1985) Factors influencing survival of vesicular-arbuscular mycorrhiza propagules during topsoil storage. *Journal of Applied Ecology* **22**, 259-266.
- Mitchell, D.J., Fullen, M.A. Trueman, I.C. & Fearnough, W. (1998) Sustainability of

- reclaimed desertified land in Ningxia, China.  
*Journal of Arid Environments* **39**, 239-251.
- Molina, R., Massicotte, H. & Trappe, J.M. (1992) Specificity phenomena in mycorrhizal symbiosis: community-ecological consequences and practical implications.  
 In: Allen, M.F. (ed.) *Mycorrhizal Functioning*. Chapman and Hall, London, 357-423.
- Moorman, T. & Reeves, F.B. (1979) The role of endomycorrhizae in revegetation practices in the semi-arid West. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations.  
*American Journal of Botany* **66**(1), 14-18.
- Moro, M.J., Pugnaire, F.I., Haase, P. & Puigdefábregas, J. (1997) Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment.  
*Functional Ecology* **11**, 425-431.
- Morrison, T.M. (1962) Absorption of phosphorus from soils by mycorrhizal plants.  
*New Phytologist* **61**, 10-20.
- Mortimore, M., Harris, F.M.A. & Turner, B. (1999) Implications of land use change for the production of plant biomass in densely populated Sahelo-Sudanian shrub-grasslands in north east Nigeria. *Global Ecology and Biogeography* **8**, 243-256.
- Moser, M. (1967) Die ectotrophe Ernährungsweise an der Waldgrenze. *Mitteilungen Forst. Bundesversuchsanst. Wien* **75**, 357-380.
- Mungongo, C. (1991) Sociological processes and land questions in the Kondoa Irangi Hills. *Ambio* **20**, 362-365.
- Munro, R.C., Wilson, J., Jefwa, J. & Mbuthia, K.W. (1999) A low-cost method of mycorrhizal inoculation improves growth of *Acacia tortilis* seedlings in the nursery.  
*Forest Ecology and Management* **113**, 51-59.
- Munyanziza, E. (1994) *Miombo Trees and Mycorrhizae: Ecological Strategies, a Basis for Afforestation*. PhD Thesis, Wageningen Agricultural University.
- Munyanziza, E., Kehri, H.K. & Bagyaraj, D.J. (1997) Agricultural intensification, soil biodiversity and agro-ecosystem function in the tropics; the role of mycorrhiza in crops and trees. *Applied Soil Ecology* **6**, 77-85.
- Munyanziza, E. & Oldeman, R.A.A. (1996) Miombo Trees: Ecological Strategies, Silviculture and Management. *Ambio*, **25**, 454-458.
- Muok, B.S., Gudu, S.O. & Odee, D.W. (1998) A broad-range inoculant for legume trees in acid soils. Fixing nitrogen in sub-Saharan Africa.  
*Agroforestry Today* (Jul-Sep), 12-13.
- Mwamba, C.K., Zgambo, Y. & Chongo, G. (1992) Effect of Seedling Source on Post-Planting Growth of *Uapaca kirkiana* Muell. Arg.  
*South African Forestry Journal* **161**, 35-40.
- Neeraj (no initial) (1992) Better uptake of nutrients in transplantation crops by inoculation of endomycorrhizal fungi and potential biological nitrogen fixing microorganisms. PhD Thesis, Kanpur University, India.
- Nemec, S., Menge, J.A., Platt, R.G. & Johnson, E.L.V. (1981) Vesicular-arbuscular mycorrhizal fungi associated with citrus in Florida and California and notes on their distribution and ecology. *Mycologia* **73**, 112-127.
- Newbery, D.M., Alexander, I.J., Thomas, D.W. & Gartlan, J.S. (1988). Ectomycorrhizal rainforest legumes and soil phosphorus in Korup National Park, Cameroon.  
*New Phytologist* **109**, 433-450.

- Newman, E.I. & Reddell, P. (1988) Relationship between mycorrhizal infection and diversity in vegetation: evidence from the Great Smoky Mountains. *Functional Ecology* **2**, 259-262.
- Newsham, K.K., Fitter, A.H. & Watkinson, A.R. (1995) Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. *Journal of Ecology* **83**, 991-1000.
- Ngalube, M.R., Hall, J.B. & Maghembe, J.A. (1995) Ecology of a miombo fruit tree: *Uapaca kirkiana* (Euphorbiaceae) *Forest Ecology and Management* **77**, 107-117.
- Ngalube, M.R., Hall, J.B. & Maghembe, J.A. (1997) Fruit, seed and seedling variation in *Uapaca kirkiana* from natural populations in Malawi. *Forest Ecology and Management* **98**, 209-219.
- Ngalube, M.R., Hall, J.B. & Maghembe, J.A. (1998) Reproductive ecology of *Uapaca kirkiana* (Euphorbiaceae) in Malawi, southern Africa. *Journal of Tropical Ecology* **14**, 743-760.
- Nix, H.A. (1983) Climate of Tropical Savannas. In: *Ecosystems of the World, Vol. 13, Tropical Savannas*. Bourliere, F. (ed.) chap.3. Elsevier, Amsterdam.
- Ojeda, R.A., Campos, C.M., Gonnet, J.M., Borghi, C.E. & Roig, V.G. (1998) The MAB Reserve of ñacuñán, Argentina : its role in understanding the Monte Desert biome. *Journal of Arid Environments* **39**, 299-313.
- Olesniewicz, K.S. & Thomas, R.B. (1999) Effects of mycorrhizal colonization on biomass production and nitrogen fixation of black locust (*Robinia pseudacacia*) seedlings grown under elevated atmospheric carbon dioxide. *New Phytologist* **142**, 133-140.
- Oliver, R., Depommier, D. & Janodet, E. (1996) Influence de *Faidherbia albida* sur le sol et le sorgho. In: CIRAD-Forêt (ed.) *Les Parcs a Faidherbia. Cahiers Scientifiques* **12**. CIRAD-Forêt, France, 141-152.
- Olson, M.E. (2001) *Moringa oleifera* Lam.  
<http://hoya.mobot.org/gradstudents/olson/oleifera.html>
- Ong, C.K. (1992) Agroforestry Databank. *Agroforestry Today* Apr-Jun, p.15.
- Ong C.K. & Leakey, R.R.B. (1999) Why tree-crop interactions in agroforestry appear at odds with tree-grass interactions in tropical savannas. *Agroforestry Systems* **45**, 109-129.
- Oppenheimer, H.R. (1957) Further observations on roots penetrating into rocks and their structure. *Bulletin of the Research Council of Israel, Section D (Botany)* **6**, 18-31.
- Otsyina, R. (1993) Would agroforestry and afforestation risk tsetse reinvasion? *Agroforestry Today* (Jan-Mar), 6-8.
- Otsyina, R., Minae, S. & Cooper, P. (1996) A never-ending story; rotational woodlots for soil conservation, wood and fodder. *Agroforestry Today* (Apr-Jun), 8-10.
- Ouedraogo S.J. (1993) The vegetative propagation of *Faidherbia albida*. The comparative evolution of the below-ground and above-ground parts of saplings grown from seedlings and cuttings. *Bois et Forêts des Tropiques* **237**, p.43.
- Ovalle, C., Aronson, J., Del Pozo, A. & Avendaño, J. (1995) Restauration et réhabilitation d'agroécosystèmes du *Secano interior* au Chile central. In: *L'homme peut-il refaire ce qu'il a défait?* Pontanier, R., M'Hiri, A., Akrimi, J., Aronson, J. & Le Floch, E. (eds.). John Libbey Eurotext, Paris, 231-245.
- Pasiecznik, N. (2001) HDRA Overseas. Tree that could bring life to the deserts.

- The Organic Way* 165, 18-19. [refers to an extension manual published 2000, and a forthcoming scientific monograph 'The *Prosopis juliflora* - *Prosopis pallida* Complex]
- Pattinson, G.S. & McGee, P.A. (1997) High densities of arbuscular mycorrhizal fungi maintained during long fallows in soils used to grow cotton except when soil is wetted periodically. *New Phytologist* 136, 571-580.
- Pons, A. (1981) The history of the Mediterranean Shrublands. In: *Ecosystems of the World, Vol. 11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L. (eds), pp.131-138. Elsevier, Amsterdam.
- Price, M. (1997) Moringa moringa everywhere ... *Agroforestry Today* (Jan-Mar), 16-17.
- Pugnaire, F.I., Haase, P., Puigdefábregas, J., Cueto, M., Clark, S.C. & Incoll, L.D. (1996) Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos* 76, 455-464.
- Puigdefábregas, J. & Mendizabal, T. (1998) Perspectives on desertification: western Mediterranean. *Journal of Arid Environments* 39, 209-224.
- Quézel, P. (1981) Floristic Composition and Phytosociological Structure of Sclerophyllous Matorral around the Mediterranean.  
In: *Ecosystems of the World, Vol. 11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L. (eds.) pp.107-121. Elsevier, Amsterdam.
- Ram, K.A., Tsunekawa, A., Sahad, D.K. & Miyazaki, T. (1999) Subdivision and fragmentation of land holdings and their implication in desertification in the Thar Desert, India. *Journal of Arid Environments* 41, 463-477.
- Reddell, P. & Warren, R. (1986) Inoculation of acacias with mycorrhizal fungi: potential benefits. In: Turnbull, J.W. (ed.) *Australian Acacias in Developing Countries*. ACIAR, Canberra. 50-53.
- Reena, J. & Bagyaraj, D.J. (1990) Response of *Acacia nilotica* and *Calliandra calothyrsus* to different VA Mycorrhizal Fungi. *Arid Soil Research and Rehabilitation* 4, 261-268.
- Reeves, F.B., Wagner, D., Moorman, T. & Kiel, J. (1979) The role of endomycorrhizae in revegetation practices in the semi-arid West. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *American Journal of Botany* 66(1), 6-13.
- Renzhong, W. & Ripley E.A. (1997) Effects of grazing on a *Leymus chinensis* grassland on the Songnen plain of north-eastern China. *Journal of Arid Environments* 36, 307-318.
- Requena, N., Jeffries, P. & Barea, J.M. (1996) Assessment of Natural Mycorrhizal Potential in a Desertified Semiarid Ecosystem. *Applied and Environmental Microbiology* 62, 842-847.
- Requena, N., Jiménez, I., Toro, M. & Barea, J.M. (1997) Interactions between plant-growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi and *Rhizobium* spp. in the rhizosphere of *Anthyllis cytisoides*, a model legume for revegetation in mediterranean semi-arid ecosystems. *New Phytologist* 136, 667-677.
- Richter, D.D. & Markewitw, D. (1995) How Deep is Soil? *BioScience* 45(9), 600-609.
- Rivas-Martínez, S. (1987) *Memoria del Mapa de Series de Vegetación de España* p.151, (published by ICONA, in conjunction with the Spanish Ministry of Agriculture).
- Rives, C.S., Bajwa, M.I. & Liberta, A.E. (1980) Effects of topsoil storage during surface mining on the viability of VA mycorrhiza. *Soil Science* 129(4), 253-257.



- Roldán, A., García, C. & Albaladejo, J. (1997) AM Fungal Abundance and Activity in a Chronosequence of Abandoned Fields in a Semiarid Mediterranean Site. *Arid Soil Research and Rehabilitation* **11**, 211-220.
- Roldán-Fajardo, B.E. (1994) Effect of indigenous arbuscular mycorrhizal endophytes on the development of six wild plants colonizing a semi-arid area in south-east Spain. *New Phytologist* **127**, 115-121.
- Rose, S.L. (1980) Mycorrhizal associations of some actinomycete nodulated nitrogen-fixing plants. *Canadian Journal of Botany* **58**: 1449-1454.
- Rose, S.L. & Youngberg, C.T. (1980) Tripartite associations in snowbush (*Ceanothus velutinus*) : effect of vesicular-arbuscular mycorrhizae on growth, nodulation and nitrogen fixation. *Canadian Journal of Botany* **59**, 34-39.
- Salvator K. (1997) Some pros and cons of *Acacia mangium*. *Agroforestry Today* (Jan-Mar), 12-13.
- Sanders, J.R. & Koide, R.T. (1994) Nutrient acquisition and community structure in co-occurring mycotrophic and non-mycotrophic old-field annuals. *Functional Ecology* **8**, 77-84.
- Sanon, K.B., Ba, A.M. & Dexheimer J. (1997) Mycorrhizal status of some fungi fruiting beneath indigenous trees in Burkina Faso. *Forest Ecology and Management* **98**, 61-69.
- Scheltema, M.A., Abbott, L.K. & Robson, A.D. (1987) Seasonal Variation in the Infectivity of VA Mycorrhizal Fungi in Annual Pastures in a Mediterranean Environment. *Australian Journal of Agricultural Research* **38**, 707-715.
- Schultka, W. & Cornelius, R. (1997) Vegetation structure of a heavily grazed range in northern Kenya: tree and shrub canopy. *Journal of Arid Environments* **36**, 291-306.
- Schwab, S. & Reeves, F.B. (1981) The role of endomycorrhizae in revegetation practices in the semi-arid west. 3. Vertical distribution of vesicular-arbuscular (VA) mycorrhiza inoculum potential. *American Journal of Botany* **68**(10), 1293-1297.
- Seghier, J. (1995) The rooting patterns of woody and herbaceous plants in a savanna; are they complementary or in competition? *African Journal of Ecology* **33**, 358-365.
- Shepherd, K.D., Jefwa, J., Wilson, J., Ndufa, J.K., Ingleby, K. & Mbuthia, K.W. (1996) Infection potential of farm soils as mycorrhizal inocula for *Leucaena leucocephala*. *Biology and Fertility of Soils* **22**, 16-21.
- Shmida, A. (1985) Biogeography of the Desert Flora. In: *Ecosystems of the World, Vol.12A, Hot Deserts and Arid Shrublands*. Evenari, M., Noy-Meir I. & Goodall, D.W. (eds.) chap.2.
- Sieverding, E. (1991) *Vesicular-Arbuscular Mycorrhiza Management in Tropical Agrosystems*, p.68. Deutsche GTZ, Eschborn.
- Sinclair, A.R.E. (1975) The resource limitation of trophic levels in tropical grassland systems. *Journal of Animal Ecology* **44**, 497-520.
- Sinclair, A.R.E. (1983) The Adaptations of African Ungulates and their Effects on Community Function. In: *Ecosystems of the World, vol.13, Tropical Savannas*. Bourliere, F.(ed.) chap.17. Elsevier, Amsterdam.
- Singh, H.P. (1998) Sustainable development of the Indian desert; the relevance of the farming systems approach. *Journal of Arid Environments* **39**, 279-284.
- Smith, S.E. & Read D.J. (1997) *Mycorrhizal Symbiosis*. Academic Press, UK.
- Smith, F.A. & Smith, S.E. (1996) Mutualism and Parasitism: Diversity in Function and Structure in the "Arbuscular" (VA) Mycorrhizal Symbiosis. *Advances in Botanical*

- Research* **22**, 1-35.
- Specht, R.L. (1981) Mallee Ecosystems in Southern Australia. In: *Ecosystems of the World, Vol.11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L.(eds.) pp.203-218. Elsevier, Amsterdam.
- Sprent, J. (2001) *Nodulation in Legumes*. RBG Kew.
- Stahl, P.D. & Christensen, M. (1991) Population variation in the mycorrhizal fungus *Glomus mosseae*: breadth of environmental tolerance. *Mycological Research* **95**, 300-307.
- Stanley, M.R., Koide, R.T. & Shumway, D.L. (1993) Mycorrhizal symbiosis increases growth, reproduction and recruitment of *Abutilon theophrasti* Medic. in the field. *Oecologia* **94**, 30-35.
- Stone, E.L. & Kalisz, P.J. (1991) On the maximum extent of tree roots. *Forest Ecology and Management* **46**, 59-102.
- Sugavanam, V., Udaiyan, K. & Devraj, P. (1998) Selection of an efficient vesicular-arbuscular mycorrhizal fungi and *Azospirillum* sp. for inoculating *Tectona grandis*. *Indian Journal of Forestry* **21**(4), 281-284.
- Sullivan, S. (1999) The impacts of people and livestock on topographically diverse open wood- and shrublands in arid north-west Namibia. *Global Ecology and Biogeography* **8**, 257-277.
- Sutherland, J. (2001) Cultivation of *M. oleifera*.  
<http://www.le.ac.uk/engineering/staff/Sutherland/moringa/cultivat/cult.htm>
- Tarafdar, J.C. & Praveen-Kumar. (1996) The role of vesicular arbuscular mycorrhizal fungi on crop, tree and grasses grown in an arid environment. *Journal of Arid Environments* **34**, 197-203.
- Thoen, D. & Bâ, A.M. (1989) Ectomycorrhizas and putative ectomycorrhizal fungi of *Azelia africana* Sm. and *Uapaca guineensis* Mull. Arg. in southern Senegal. *New Phytologist* **113**, 549-559.
- Thomas, D.S.G. (1997) Science and the desertification debate. *Journal of Arid Environments* **37**, 599-608.
- Thompson, J.P. (1987) Decline of Vesicular-Arbuscular Mycorrhizae in Long Fallow Disorder of Field Crops and its Expression in Phosphorus Deficiency of Sunflower. *Australian Journal of Agricultural Research* **38**, 847-867.
- Thompson, J.P. (1990) Soil sterilization methods to show VA-mycorrhizae aid P and Zn nutrition of wheat in vertisols. *Soil Biology and Biochemistry* **22**(2), 229-240.
- Thompson, J.P. (1994) Inoculation with vesicular-arbuscular mycorrhizal fungi from cropped soil overcomes long-fallow disorder of linseed (*Linum usitatissimum* L.) by improving P and Zn uptake. *Soil Biology and Biochemistry* **26**(9), 1133-1143.
- Tiffen, M., Mortimore, M. & Gichuki, F. (1994, re-printed 1997) *More People, Less Erosion: Environmental Recovery in Kenya*. John Wiley & Sons, Chichester.
- Tomaselli, R. (1981) Main Physiognomic Types and Geographic Distribution of Shrub Systems Related to Mediterranean Climates. In: *Ecosystems of the World, Vol.11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L.(eds.) 95-106. Elsevier, Amsterdam.
- Tomlinson, H., Teklehaimanot, Z., Traoré A. & Olapade, E. (1995) Soil amelioration and root symbioses of *Parkia biglobosa* (Jacq.) Benth. in West Africa. *Agroforestry Systems* **30**, 145-159.

- Tommerup, I.C. (1983) Spore dormancy in vesicular-arbuscular mycorrhizal fungi. *Transactions of the British Mycological Society* **81**, 37-45.
- Tommerup, I.C. & Abbott, L.K. (1981) Prolonged survival and viability of VA mycorrhizal hyphae after root death. *Soil Biology and Biochemistry* **13**, 431-433.
- Toro, M., Azcón, R. & Barea, J.M. (1997) Improvement of Arbuscular Mycorrhiza Development by Inoculation of soil with Phosphate-Solubilizing Rhizobacteria to Improve Rock Phosphate Availability ( $^{32}\text{P}$ ) and Nutrient Cycling. *Applied and Environmental Microbiology* **63**, 4408-4412.
- Trabaud, L. (1981) Man and Fire; Impacts on Mediterranean Vegetation. In: *Ecosystems of the World, Vol.11, Mediterranean-type Shrublands*. di Castri, F., Goodall, D.W. & Specht, R.L. (eds.) pp. 523-537. Elsevier, Amsterdam.
- Trapnell, C.G. (1959) Ecological results of woodland burning experiments in Northern Rhodesia. *Journal of Ecology* **47**, 129-168.
- Trapnell, C.G., Friend, M.T., Chamberlain, G.T. & Birch, H.F. (1976) The effects of fire and termites on a Zambian woodland soil. *Journal of Ecology* **64**, 577-588.
- UNEP World Atlas of Desertification (1992) Edward Arnold. Nairobi/London.
- van der Hammen, T. (1983) The Palaeoecology and Palaeogeography of Savannas. In: *Ecosystems of the World, vol.13, Tropical Savannas*. Bourliere, F. (ed.) chap.2. Elsevier, Amsterdam.
- van der Heijden, E.W. & Vosatka, M. (1999) Mycorrhizal associations of *Salix repens* L. communities in succession of dune ecosystems. II. Mycorrhizal dynamics and interactions of ectomycorrhizal and arbuscular mycorrhizal fungi. *Canadian Journal of Botany* **77**, 1833-1841.
- Varma, A. (1995) Ecophysiology and Application of Arbuscular Mycorrhizal Fungi in Arid Soils. In: *Mycorrhiza*. Varma, A. & Hock, B. (eds.) Springer-Verlag, Berlin/Heidelberg.
- Vashishtha, B.B. (1997) Ziziphus for drylands – a perennial crop solving perennial problems. *Agroforestry Today* Jul-Sep, 10-12.
- Vesey-Fitzgerald, D.F. (1963) Central African grasslands. *Journal of Ecology* **51**, 243-274.
- Virginia, R., Jenkins, M.B. & Jarrell, W.M. (1986) Depth of root symbiont occurrence in soil. *Biology and Fertility of Soils* **2**, 127-130.
- Visser, S., Griffiths, C.L. & Parkinson, D. (1984) Topsoil storage effects on primary production and rates of vesicular-arbuscular mycorrhizal development in *Agropyron trachycaulum*. *Plant and Soil* **82**, 51-60.
- Vivekanandan, P. (1998) New tree, new system: neem production in South India. *Agroforestry Today*, Jan-Mar, 12-14.
- Warner, N.J., Allen, M.F. & MacMahon, J.A. (1987) Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. *Mycologia* **79**(5), 721-730.
- West, N.E. (ed.) (1983) *Ecosystems of the World, Vol.5, Temperate Deserts and Semi-deserts*, p.4. Elsevier, Amsterdam.
- Wickens, G.E. (1998) *Ecophysiology of Economic Plants in Arid and Semi-Arid Lands*. Springer, Berlin.
- Wilcox, H.E. (1996) Mycorrhizae; in *Plant Roots – the Hidden Half*, 2<sup>nd</sup> edition, Yoav Waisel *et al* (ed.) Marcel Dekker Inc., New York.
- Zaafouri, M.S., Akrimi, N., Floret, Ch., Le Floc'h, E. & Pontanier, R. (1995) Les arbustes

fourragers exotiques. Leur intérêt pour la réaffectation des terres dégradées des régions arides et désertiques tunisiennes. In: Pontanier R., M'Hiri, A., Akrimi, N., Aronson J. & Le Floch, E. (eds.) *L'homme peut-il refaire ce qu'il a défait?*

John Libbey Eurotext, Paris.

Zajicek, J.M., Hetrick, B.A.D. & Owensby, C.E. (1986) The influence of soil depth on mycorrhizal colonization of forbs in the tallgrass prairie. *Mycologia*, **72**(2), 316-320.

Zha, Y. & Gao, J. (1997) Characteristics of desertification and its rehabilitation in China. *Journal of Arid Environments* **37**, 419-432.

## **Appendix 1 - Protocol for simple, low-cost mycorrhizal inoculation**

- based on work done in Kenya, described by Munro *et al* (1999)\*.

**Initial assumptions:** Most healthy natural vegetation maintains mutually beneficial relationships with mycorrhizal soil fungi. These relationships are likely to be particularly important in nutrient-poor soils subject to drought. But populations of mycorrhizal fungi will be badly depleted in desertified land; in cultivated land they may still be abundant, but will probably be different in type. So young trees or shrubs transplanted into such conditions will benefit from inoculation with suitable fungal partners.

In areas where healthy trees or shrubs of the same or similar species still grow, the best simple, cheap source of suitable inoculum is likely to be the root zone of these trees. But there is an obvious limit to the amount of soil and fine roots that can be gathered without damaging the tree, and in any case the inoculum gathered may not be very concentrated, so the following method for culturing and multiplying it is recommended.

### **Method:**

1. Collect soil from beneath<sup>1</sup> several healthy mature trees<sup>2</sup>.

2. Sow seeds of a suitable bait plant<sup>3</sup> into this soil immediately and grow the plants for at least 6 weeks in good light<sup>4</sup>. Keep the containers on a clean bench to avoid contamination.
3. Pregerminate the tree seed after scarification if necessary. This procedure needs to be timed so that germination coincides with the harvesting of inoculum (stage 4).
4. Harvest the bait plants – cut off tops, wash and chop up roots into 1 cm lengths. Mix these root fragments with the soil in which the bait plants grew. This mixture is the inoculum<sup>5</sup>.
5. Part-fill containers with soil from under herbaceous vegetation<sup>6</sup>.
6. Add 25 ml of fresh inoculum.
7. Sow pre-germinated tree seeds onto the inoculum.
8. Cover seeds with fine soil or sand.
9. Label, water and keep on a bench in good light, giving usual nursery care.

**Footnotes:**

<sup>1</sup> In the absence of precise information, it would be prudent to take both topsoil from near the edge of the canopy and some soil from deeper nearer trunk.

<sup>2</sup> Choice of source tree – ideally the same species or one as closely related or similar as possible. If the seedlings to be inoculated are legumes, the source tree should also be a legume.

<sup>3</sup> Choice of bait plant – many common plants are suitable; maize or other Poaceae, annual legumes, leeks or onions are good. If the target trees are legumes, some at least of the bait plants should be annual legumes. The cabbage (Brassicaceae) or beet (Chenopodiaceae) families are not suitable as bait plants.

<sup>4</sup> The Munro team harvested the bait plant (maize and cowpea) roots + soil after only 6 weeks, and for practical reasons the shorter time needed the better. But some reports state that infectivity is highest at flowering time, and onions only flower in their second season. More research is needed on the selection of host plant species and on how long the trap-pot culture needs to be grown for.

<sup>5</sup> If the inoculum is not needed when the bait plants are ready, it can be harvested and re-sown with a second generation of bait plants. This will produce a larger amount of inoculum at a later date.

<sup>6</sup> If this is not practicable or suitable, a peat-sand mix, coir or other similar substrate can be used, in which case the proportion of inoculum should be doubled. The mixture must not be rich in phosphate (30 ppm P is the maximum recommended).

- Munro, R.C., Wilson, J., Jefwa, J. & Mbuthia, K.W. (1999) A low-cost method of mycorrhizal inoculation improves growth of *Acacia tortilis* seedlings in the nursery.

*Forest Ecology and Management* **113(3)**, 51-56.

## Appendix 2 - Suggestions for further research

1. Test the assumptions on timing of procedures contained in the Protocol.
  
2. Test for possible special role of AMF species known to function at great depths. The format might be to carry out the range of inoculation treatments listed below with both *Faidherbia albida* and *Acacia tortilis* ssp. *raddiana*.
  1. Control (sterilized soil)
  2. + *Rhizobium*
  3. + *Rhizobium* + wild inoculum
  4. + *Glomus fasciculatum*
  5. + *G. fasciculatum* + *Rhizobium*
  6. + *G. fasciculatum* + *Rhizobium* + wild inoculum
  7. + *Gigaspora margarita*
  8. + *Gi. margarita* + *Rhizobium*
  9. + *Gi. margarita* + *Rhizobium* + wild inoculum
  10. + *G. fasciculatum* + *Gi. margarita* + *Rhizobium* + wild inoculum.
  
3. The striking results reported with Tagasaste in Section 4.3.2. suggest that this legume may be compatible with a range of rhizobial partners. The hypothesis of Aronson and associates (4.3.1.) could be tested by comparing sample patches:
  - (a) seeded with Tagasaste or a local annual medick in year one and outplanted with mycorrhizal woody legumes in year two,

(b) outplanted with mycorrhizal woody legumes in year one, followed by seeding with Tagasaste or a local annual medick in year two,

(c) seeded and outplanted simultaneously with both (a) and (b) in year one.

Apart from the survival and growth of the plants, research questions would ask whether the mycorrhizal inocula were maintained in the field, whether the medicks or tagasaste were nodulated by wild inoculum present, and if not, whether a more effective *Rhizobium* could be obtained and added at inoculation stage.

4. The AM to EM sequence seen in *Uapaca kirkiana* could be investigated by germinating seed in AM inoculum and outplanting the seedlings into planting holes lined with EM inoculum.
5. The response of tree seedlings to mycorrhizal + phosphate-solubilizing bacteria, with/without added rock phosphate would be interesting, particularly in a rock-phosphate-producing area of Burkina Faso or Tanzania. A variant in SE Spain could be the outplanting of clumps of mycorrhizally inoculated *Argania spinosa* or *Tetraclinis articulata* with/without rock phosphate and phosphate-solubilizing bacteria added at outplanting time.